The Late Triassic (Norian) Adamanian–Revueltian tetrapod faunal transition in the Chinle Formation of Petrified Forest National Park, Arizona

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ABSTRACT: Recent stratigraphic revisions of the Upper Triassic Chinle Formation of Petrified Forest National Park, in conjunction with precise and accurate documentation of fossil tetrapod occurrences, clarified the local biostratigraphy, with regional and global implications. A significant overlap between Adamanian and Revueltian faunas is rejected, as is the validity of the Lamyan sub-land vertebrate faunachron. The Adamanian–Revueltian boundary can be precisely placed within the lower Jim Camp Wash beds of the Sonsela Member and thus does not occur at the hypothesised Tr-4 unconformity. This mid-Norian faunal turnover, may coincide with a floral turnover, based on palynology studies and also on sedimentological evidence of increasing aridity. Available age constraints bracketing the turnover horizon are consistent with the age of the Manicouagan impact event. The rise of dinosaurs in western North America did not correspond to the Adamanian–Revueltian transition, and overall dinosauromorph diversity seems to have remained at a constant level across it. The paucity of detailed Late Triassic vertebrate biostratigraphic data and radioisotopic dates makes it currently impossible to either support or reject the existence of globally synchronous Late Triassic extinctions for tetrapods.

KEY WORDS: Biochronology, biostratigraphy, extinction, Manicouagan, Sonsela Member

A principal goal of the biostratigrapher is to utilise fossil occurrences in conjunction with the superpositional relationships of the strata containing these occurrences, to reconstruct the succession of extinct organisms. Of particular interest to the biostratigrapher is the appearance and disappearance of various taxa, because this provides the basis for faunal zonations that can be used to correlate discontinuous strata locally, regionally and, in some cases, globally (e.g. McGowran 2005; Woodburne 2006). Though vertebrate biostratigraphy was historically used as an important method for inferring chronologically equivalent strata in different areas (e.g. Lucas 1998; Lindsay 2003; Woodburne 2006), it is also an important tool for relating the evolution and extinction of taxa to each other and to changing environmental conditions (e.g. Case 1996). Moreover, it can be used to establish whether multiple taxa disappear in roughly the same stratigraphic interval, possible evidence for an extinction event (e.g. Benton 1994a).

Constructing a robust biostratigraphy relies chiefly on determining the correct superpositional relationships of fossil-bearing strata. Errors in lithostratigraphic correlation can heavily influence biostratigraphic inferences. For example, miscorrelating units in different stratigraphic sections can make taxa with distinct ranges appear to have overlaps (Fig. 1a–b). Alternately, if the stratigraphic ranges of different taxa actually overlap, but are not currently known from the same locality, miscorrelation can make them appear to have distinct ranges (Fig. 1c–d). Also crucial is the ability to know in which particular strata fossil localities occur, to allow precise determination of stratigraphic ranges. This requires that the exact geographic placement of localities be determined so that the strata they occur in can be accurately identified (McKenna & Lillegraven 2005). Additionally, it is important to recognise whether taxa have sample sizes large enough to provide a reliable estimate of stratigraphic range (Marshall 1998; McKenna & Lillegraven 2005). Finally, it is important to use only specimens that have reliable taxonomic assignments based on the presence (or absence) of discrete character states (e.g. Bell *et al.* 2004, 2010; Bever 2005; Nesbitt *et al.* 2007; Nesbitt & Stocker 2008).

Despite over 150 years of study, the stratigraphic distribution of fossils in Upper Triassic deposits of the southwestern United States is still not well-understood. Despite the extensive use of Upper Triassic vertebrate fossils as biochronologic indicators for these strata (e.g. Lucas & Hunt 1993; Lucas *et al.* 1997, 2007a; Lucas 2010), the stratigraphic resolution of these studies has remained coarse. To date, only two studies (Parker 2006; Martz 2008) have attempted to accurately relocate and plot all known Upper Triassic vertebrate fossil localities in particular study areas in western North America with a high degree of precision in order to determine the exact stratigraphic ranges of taxa. Parker's (2006) study of the Chinle Formation in Petrified Forest National Park (PEFO) in northeastern Arizona (Fig. 2) based its biostratigraphic model on a lithostratigraphic scheme (Heckert & Lucas 2002a; Woody 2006) that was later shown to be erroneous (Raucci *et al.* 2006; Martz & Parker 2010), and Martz's (2008) results remain unpublished.

The modified lithostratigraphic model for PEFO (Martz & Parker 2010, unpublished data), in conjunction with a steadily
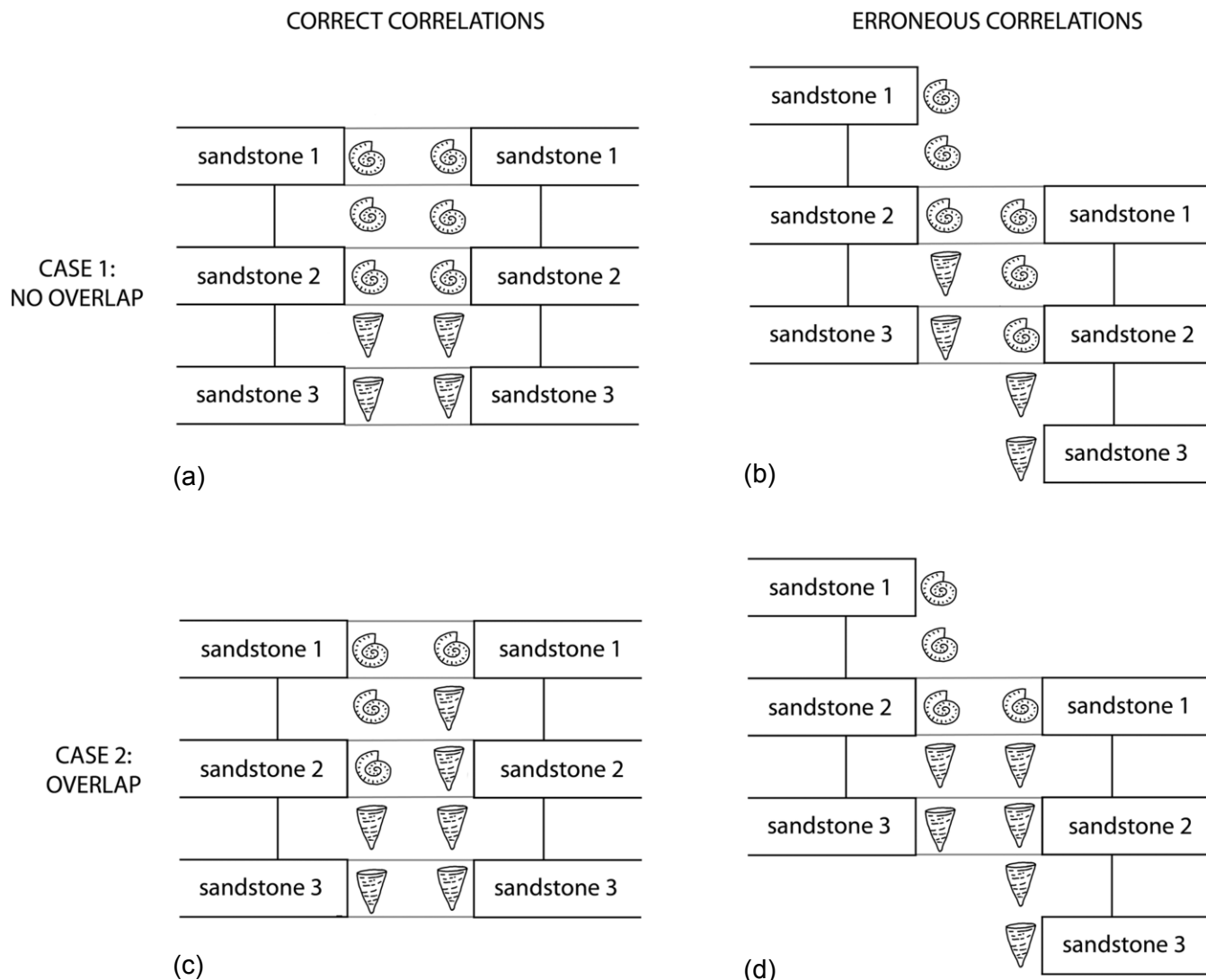
CORRECT CORRELATIONS

ERRONEOUS CORRELATIONS

CASE 1: NO OVERLAP

(a)

(b)

CASE 2: OVERLAP

(c)

(d)

Figure 1 Hypothoetical erroneous comparisons of biostratigraphic ranges resulting from mistakes in lithostratigraphic correlation. Two stratigraphic columns from different localities are shown side by side, with known fossil occurrences from the localities shown next to their respective columns. In cases where two taxa have non-overlapping ranges (a), errors in correlation can make it appear that the ranges overlap (b). In cases where two taxa have overlapping ranges but are not known from the same locality (c), errors in correlation can make it appear that the ranges do not overlap (d).

increasing sample of vertebrate fossils, allows for a reexamination of the park biostratigraphy. Comparison of detailed biostratigraphic models with sedimentological data from the same strata allows patterns of vertebrate faunal change to be compared to changes in the environment, particularly palaeoclimate. Moreover, an increasing number of available radioisotopic dates (e.g. Riggs *et al.* 2003; Irmis & Mundil 2008; Ramezani *et al.* 2009; Heckert *et al.* 2009) allows a more accurate and precise calibration of the Chinle Formation to the geochronologic time scale.

The objective of this study is to use detailed biostratigraphic data to examine critically a purported stratigraphic overlap between two vertebrate faunas within the Chinle Formation of PEFO (Woody & Parker 2004; Hunt *et al.* 2005a; Parker 2006), evaluate the relationship between the faunal turnover and environmental changes, reassess the geochronologic age of the Adamanian and Revueltian biozones and that of the transition between them, and to appraise the extent to which this biostratigraphic transition may be correlated geochronologically to other events across Late Triassic Pangea.

Institutional abbreviations: AMNH, American Museum of Natural History, New York, NY; CFMNH (PR), Field Museum of Natural History, Chicago; IL; PEFO, Petrified

Forest National Park Museum Collections, Petrified Forest National Park, AZ; NMMNH, New Mexico Museum of Natural History and Science, Albuquerque, NM; NMMNHS, New Mexico Museum of Natual History and Science fossil locality; PFP, Petrified Forest National Park Plant Locality; PFV, Petrified Forest National Park Vertebrate Locality; TMM, Texas Memorial Museum Vertebrate Paleontology Laboratory, Austin, TX; UCMP, University of California Museum of Paleontology, Berkeley, CA; USNM, United States National Museum, Washington, DC.

1. Previous work

1.1. Lithostratigraphy
PEFO preserves one of the thickest and most easily accessible exposures of the Chinle Formation. Accordingly, the geology and palaeontology of the park are well studied, resulting in over 700 technical papers, theses and abstracts (see Long & Murry 1995; Heckert *et al.* 2005; Martz & Parker 2010 for summaries). Stewart *et al.* (1972) provided a detailed summary of Chinle Formation lithostratigraphy across the Colorado Plateau, and Cooley (1958), Roadifer (1966), Billingsley
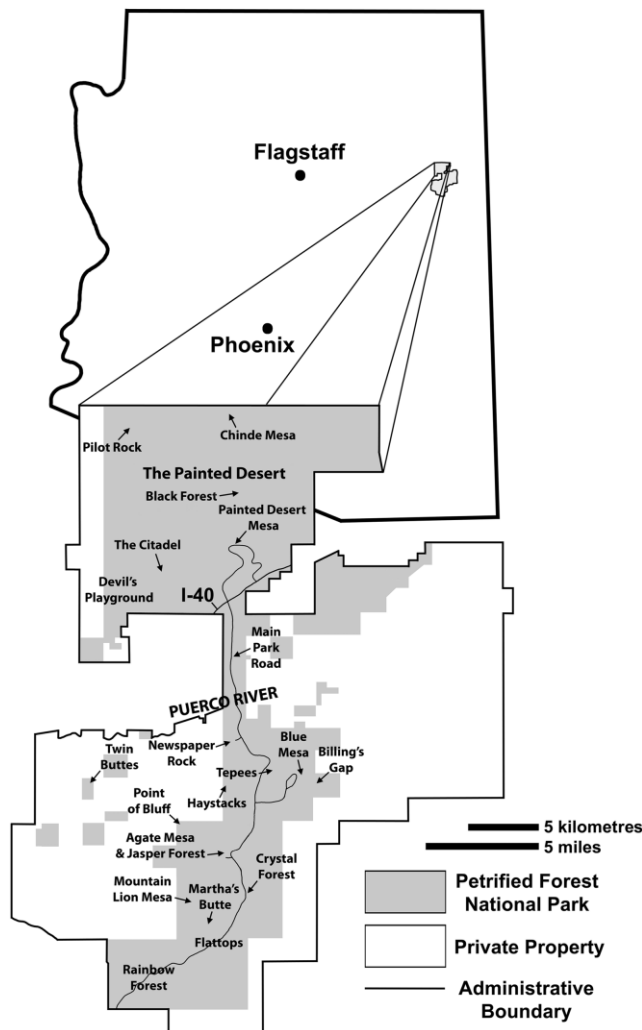
Figure 2 Map of Petrified Forest National Park, showing important geographic regions and landmarks.

(1985), Ash (1987), Murry (1990), Heckert & Lucas (2002a) and Woody (2006) conducted more focused published studies of PEFO and surrounding area. Most work in Petrified Forest National Park between 1985 and 2002 used Billingsley's (1985) lithostratigraphic model and accompanying map (e.g. Long & Murry 1995; Therrien & Fastovsky 2000), or a version with nomenclatural modifications (i.e., Chinle Group instead of Chinle Formation; e.g. Lucas 1993; Steiner & Lucas 2000). Heckert & Lucas (2002a) and Woody (2003, 2006) provided significant revisions to this scheme that were subsequently modified by Martz & Parker (2010), as discussed below.

Approximately 10 kilometres of surface exposures divide outcrop exposures in the park into two distinct areas north and south of the Puerco River. The southern portion contains the major fossil 'forests' of petrified logs (from north to south the Blue, Jasper, Crystal and Rainbow Forests). The northern portion consists of the Painted Desert (including the Black Forest) and Devils Playground areas. Lithostratigraphic correlation between these areas is difficult, with several hypotheses currently proposed (e.g. Roadifer 1966; Billingsley 1985; Therrien & Fastovsky 2000; Heckert & Lucas 2002a).

1.2. Biostratigraphy

It was long recognised that there are stratigraphically distinct faunas (i.e. a group of animals with a particular geographic and temporal range, *sensu* Tedford 1970, pp. 679–680) in Upper Triassic strata in the western United States, and phyto-

saurs were historically considered to be the most important index taxa for defining these faunas (Camp 1930; Colbert & Gregory 1957; Gregory 1957, 1972; Long & Ballew 1985; Long & Padian 1986; Chatterjee 1986; Hunt & Lucas 1991; Long & Murry 1995). Camp (1930) was the first to recognise that variation in the temporal region of phytosaurs, particularly in the morphology of the squamosal, could be used for biostratigraphy. Camp (1930) identified distinct phytosaur morphotypes (by which we mean fossil organisms or parts of fossil organisms sharing a distinctive morphology that may be taxonomically significant) occurring below and above the sandstone unit in northeastern Arizona that was later named the Sonsela sandstone bed (now called the Jasper Forest bed; Akers *et al.* 1958; Raucci *et al.* 2006; Martz & Parker 2010). Gregory (1957, 1972) and Colbert & Gregory (1957) identified four consecutive faunas in Upper Triassic strata across the western United States that were characterised largely by distinct phytosaur morphotypes. They noted that the middle two faunas (Fig. 3) were present in northeastern Arizona and corresponded to Camp's upper and lower faunas. Long & Ballew (1985) were the first to fully utilise aetosaurs for biostratigraphy and confirmed, along with Long & Padian (1986), the existence of two faunas in the Chinle Formation of PEFO characterised by particular phytosaur and aetosaur taxa, separated by the Jasper Forest bed. These various workers also recognised that metoposaurs and dicynodonts occurred primarily in the lower fauna.

Lucas (1991, 1993) was the first to treat the four faunas of Gregory (1957; Colbert & Gregory 1957) as biochronologic units with the intent of developing a provincial system of Late Triassic biochronology for western North America in the pattern of Cenozoic mammalian biochronology (Lucas 1990; see Tedford 1970; Woodburne 1996, 2004 for a discussion of the following terms and concepts). Lucas & Hunt (1993) formalised these biochronologic units as the 'Late Triassic land vertebrate faunachrons (lvfs)', naming the middle two the Adamanian and Revueltian lvfs, corresponding to the lower and upper faunas in PEFO, respectively. Subsequent authors attempted to support and refine these faunachrons (e.g. Lucas & Heckert 1996a; Heckert & Lucas 1997a; Hunt *et al.* 1998a, b, 2005a; Lucas 1998, 2010; Lucas *et al.* 2007). One of the most important refinements was redefining the faunachrons based on the FADs (first appearance datums) of phytosaur taxa (Lucas 1998), with the beginning of the Adamanian and Revueltian defined by the FADs of the phytosaurs *Rutiodon* (southwestern US occurrences of '*Rutiodon*' are currently assigned to *Leptosuchus*, but see discussion below) and *Pseudopalatus*, respectively. The feasibility of attempts to use these faunachrons for global biochronology (e.g. Lucas 1998, 2010; Lucas & Heckert 2000; Lucas *et al.* 2007a) is debated, with the general consensus that the Adamanian and Revueltian faunachrons may be applicable within western North America, but that they probably cannot be precisely correlated to other parts of the world (Langer 2005; Rayfield *et al.* 2005, 2009; Schultz 2005; Parker 2006; Irmis *et al.* 2010).

Following stratigraphic revisions of the Chinle Formation in Petrified Forest National Park by Heckert & Lucas (2002a) and Woody (2003, 2006), Woody & Parker (2004) suggested that there is a partial stratigraphic overlap of Adamanian and Revueltian index taxa. In response to this and another interpreted overlap of Adamanian and Revueltian taxa in eastern New Mexico (Hunt & Lucas 2005), Hunt *et al.* (2005a) subdivided the Adamanian into two sub-lvfs, the older St Johnsian and younger Lamyan (in which the overlap purportedly occurred). The Lamyan was defined by the FAD of the aetosaur *Typothorax antiquum*, and the beginning of the
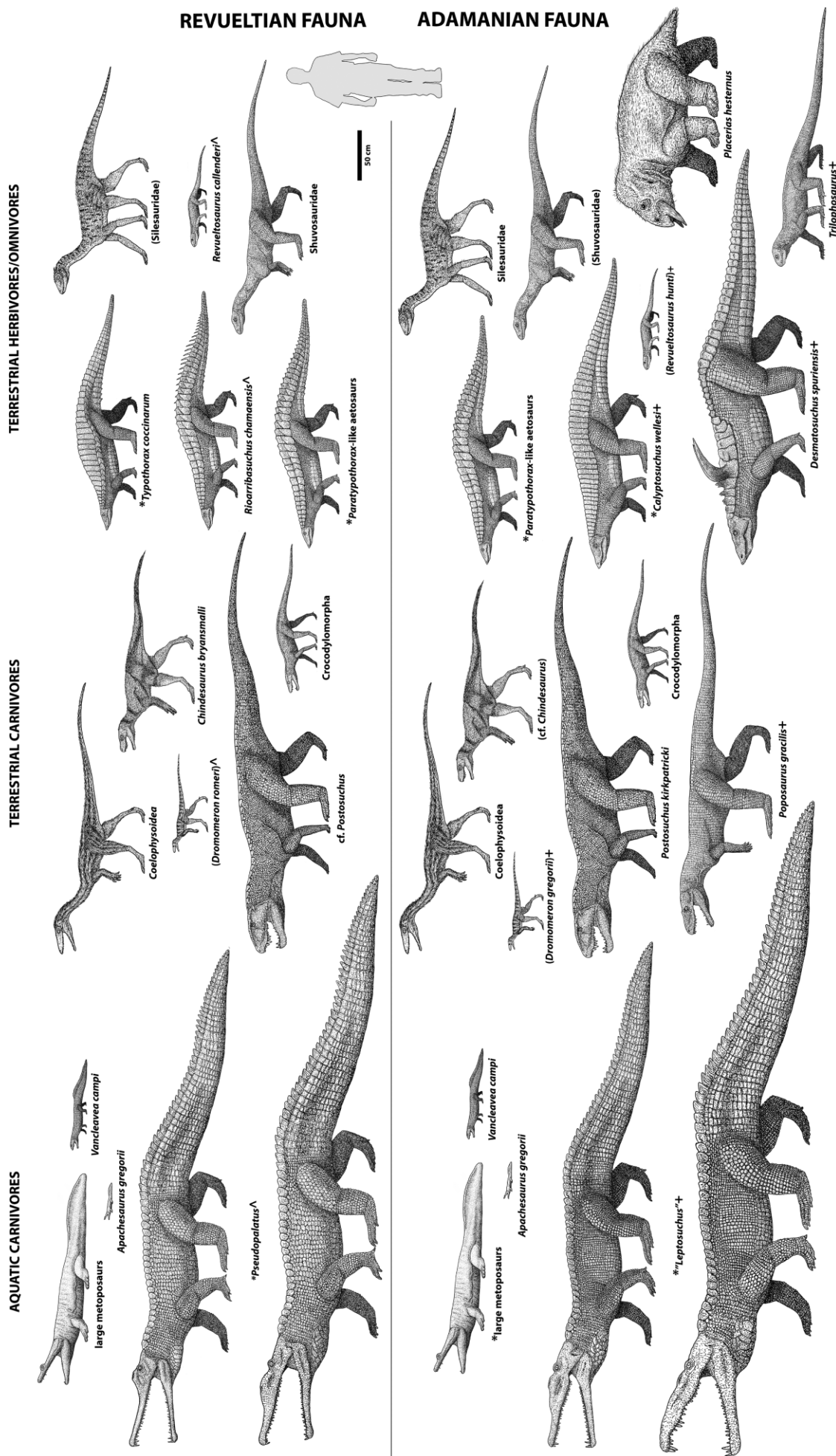
Figure 3 The Adamanian and Revueltian tetrapod faunas from northern Arizona. Taxa marked with an asterisk (*) represent the most frequently encountered fossils for those faunas; taxa in the Adamanian fauna marked with a cross (+) do not occur in the Revueltian fauna; Revueltian taxa marked with an arrow (^) do not occur in the Adamanian fauna; taxa in parentheses are not known from the Adamanian and Revueltian faunas within the park, but occur in the faunas in the Chinle Formation outside the park. Particularly small tetrapods (e.g. sphenodonts, drepanosaurs, procolophonids) are excluded, as they would be barely visible and are unknown from PEFO.

Revueltian was redefined as the FAD of *Typothorax cocci-narum* because of the alleged extension of *Pseudopalatus* into the Lamyan. Parker (2006) debated the validity of these sub-lvfs, based on objections to the distinctiveness of *Typothorax antiquum* from *T. coccinarum*. He also noted that because the lvfs are defined using FADs, there was no need for these revised definitions; the base of the Revueltian simply moved down with the apparently low occurrence of *Pseudopalatus*.

Parker (2006) plotted fossil occurrences onto a composite stratigraphic column for the Petrified Forest and demonstrated a purported Lamyan faunal overlap of Adamanian and Revueltian index taxa; however, he cautioned that the overlap was due solely to stratigraphic correlation and that Adamanian and Revueltian index taxa had never been recovered together in any particular quarry (Parker 2006, p. 58). Raucci *et al.* (2006) and subsequently Martz & Parker (2010) discussed problems with the lithostratigraphic correlations of Heckert & Lucas (2002a) and Woody (2003, 2006) within the Sonsela Member. The most significant of these was miscorrelation of the Jasper Forest bed with the Flattops One sandstones, and also the miscorrelation of the Jim Camp Wash beds with the Lot's Wife beds (*sensu* Martz & Parker 2010). The ramifications of these lithostratigraphic revisions for the Lamyan faunal overlap is dealt with in this present paper.

2. Methods

2.1. Fieldwork
Physically tracing out and mapping all pertinent lithostratigraphic units, as well as measuring numerous stratigraphic sections, resulted in a revised, detailed and testable lithostratigraphic model for the Chinle Formation in the southern part of Petrified Forest National Park (Fig. 4; Martz & Parker 2010). The same techniques were used to correlate and map major beds in the northern region of the park (Devil's Playground and the Painted Desert; Fig. 5), as well as proposed revised lithostratigraphic correlations between the northern and southern regions of the park, allowing a composite lithostratigraphic column (Fig. 6) to be provided for the Chinle Formation throughout the entire park. The lithostratigraphy of the northern region, and the correlations between the southern and northern regions, will be fully described in another publication.

Recent fieldwork in PEFO has resulted in the documentation of over 300 fossil localities and the collection of numerous specimens (e.g. Parker & Clements 2004; Stocker *et al.* 2004; Parker & Irmis 2005). These include some localities from the 2004 park boundary expansion (Fig. 2). These data add to nearly 200 already existing localities documented by previous workers (e.g. Long & Ballew 1985; Long & Murry 1995; Hunt *et al.* 1996; Parker 2002). Precise placement of sites within the new stratigraphic framework allows for the construction of detailed range charts for all taxonomically diagnostic specimens (Figs 4–6). Previous attempts to place localities in stratigraphic position (e.g. Heckert & Lucas 2002a) contained errors, mainly because maps used to provide these data (Billingsley 1985; Evanoff 1994) contain inaccuracies. The present authors also were able to relocate the pollen localities of Litwin (1986; Litwin *et al.* 1991) and plot these on the stratigraphic model.

Because exposures in the northern and southern parts of the park are discontinuous, potentially correlative units in these areas historically were given different names; separate detailed biostratigraphic plots for these areas are presented, along with a composite biostratigraphic range chart plotted on the composite lithostratigraphic column. All data pertinent to this study, including measured sections and fossil locality information, are available at PEFO to approved researchers.

2.2. The treatment of the Late Triassic land vertebrate 'faunachrons' as biostratigraphic units
Vertebrate biochrons are often treated as abstract units of time completely liberated from the stratigraphic record (Berggren & Van Couvering 1974, p. 7; Walsh 1998; Lucas 1998). However, this is misleading, because biochronology is derived entirely from stratigraphic information, making detailed and accurate biostratigraphy essential for a reliable biochronologic system (e.g. Tedford 1970; Emry 1973; Woodburne 1996, 2006). Because of the wish to emphasise the dependency of the Adamanian and Revueltian 'land vertebrate faunachrons' on empirically determined biostratigraphic data affected by collecting biases and an incomplete fossil record, they are treated here as biostratigraphic rather than biochronologic units; in other words, as units of rock defined by fossil occurrences rather than as units of time (Salvador 1994; Walsh 1998).

Consequently, the boundary definitions of Lucas (1998) using the FADs (first appearance datum) of the phytosaur taxa '*Leptosuchus*' and *Pseudopalatus* are modified to be based on empirically determined biostratigraphic data. Instead of FADs, which are biochronologic datums (Woodburne 2004), lowest known stratigraphic occurrences ('LSD$_k$s' *sensu* Walsh 1998 = 'LSDs' *sensu* Woodburne 2004) are used to mark the lower boundary of each biozone, making them 'lowest occurrence interval biozones' (*sensu* Salvador 1994). Although it would be more correct to refer to these biozones as the '*Leptosuchus*'/*Pseudopalatus* lowest occurrence interval zone'' (for the Adamanian) and '*Pseudopalatus*/*Redondasaurus* lowest occurrence interval zone' (for the Revueltian), the less cumbersome terminology 'Adamanian biozone' and 'Revueltian biozone' is preferred.

3. Taxonomic considerations

Overviews of the Chinle fauna and flora from PEFO were provided by Long & Murry (1995), Parker (2005a), Irmis (2005) and Ash (2005). In the following sections vertebrate and plant localities in PEFO are designated by the prefixes PFV and PFP, respectively. When referred specimens establish stratigraphic ranges, specimen numbers for voucher specimens are given as recommended by Nesbitt & Stocker (2008). All specimens listed by Long & Murry (1995) from the UCMP collections were taxonomically reevaluated, and specimens that could not be relocated to confirm their taxonomic assignments are not included in this study. Thus, this taxonomic list for localities and horizons differs from that of Long & Murry (1995).

Most of the vertebrate specimens recovered at PEFO are fragmentary, and many are too incomplete to be assigned definitively to particular species, or even genera. In addition to plotting ranges for alpha taxa, ranges are also plotted for some higher clades and paraphyletic grades distinguished by particular suites of morphological characters. Moreover, the alpha taxonomy of many groups is controversial, and the criteria for the referral of specimens require further discussion in the following sections.

3.1. *Typothorax*
The aetosaur *Typothorax coccinarum* (Fig. 7a–b) is diagnosed primarily by a combination of paramedian osteoderm characters, including a raised anterior bar, high maximum width/length ratios (4:1 or higher), a thick ventral strut and

Figure 4 Lithostratigraphic section and known biostratigraphic ranges of tetrapod taxa in the southern part of Petrified Forest National Park. 'X's represent known occurrences of taxa, grey bars the known range. Occurrences of particular interest are designated with numbers, and explained at the bottom of the figure.
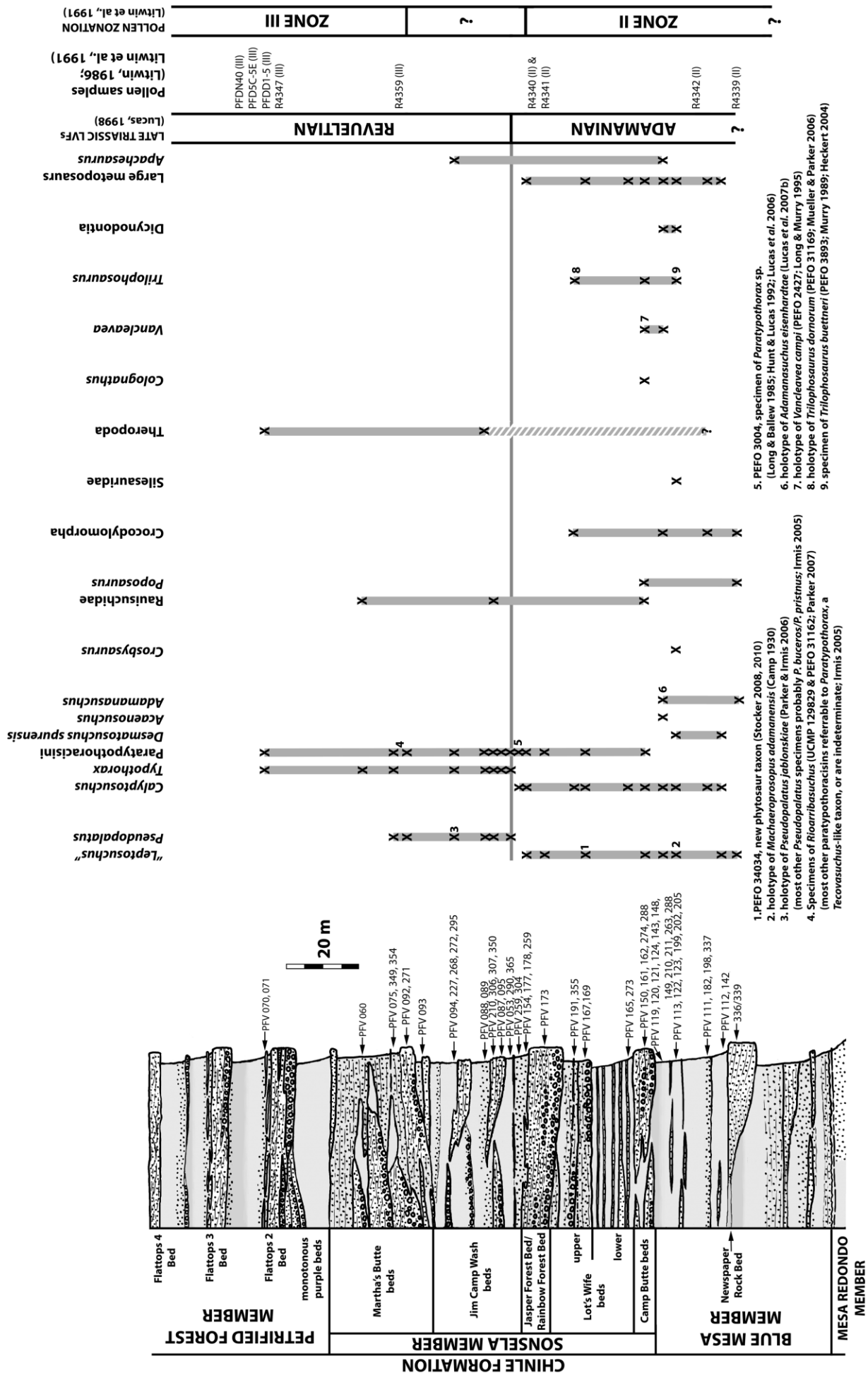
Figure 5 Lithostratigraphic section and known biostratigraphic ranges of tetrapod taxa in the northern part of Petrified Forest National Park. 'X's represent known occurrences of taxa, grey bars the known range. Occurrences of particular interest are designated with numbers, and explained at the bottom of the figure.
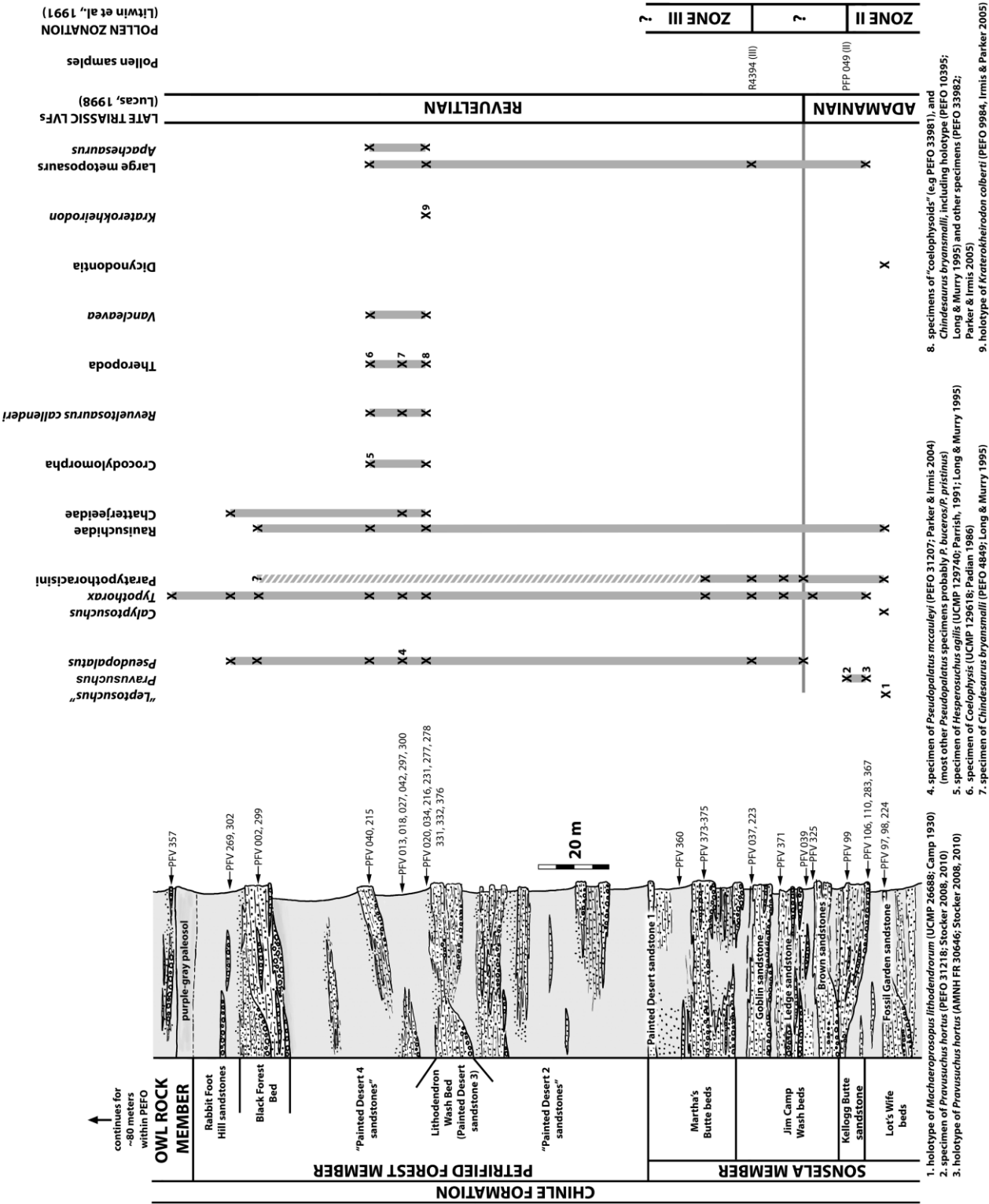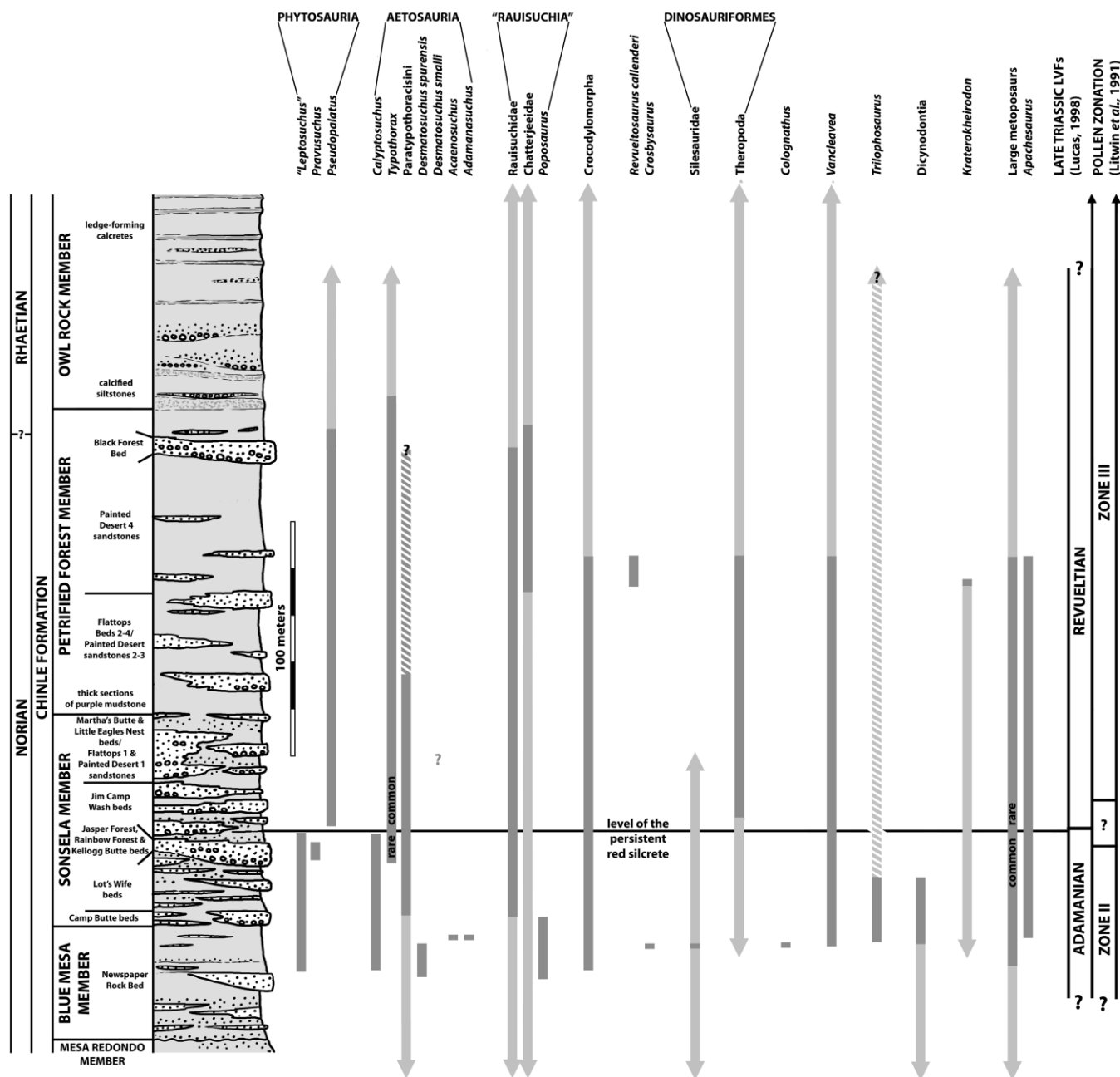
1. holotype of *Machaeroprosopus lithodendrorum* (UCMP 26688; Camp 1930)
2. specimen of *Pravusuchus hortus* (PEFO 31218; Stocker 2008, 2010)
3. holotype of *Pravusuchus hortus* (AMNH FR 30646; Stocker 2008, 2010)
4. specimen of *Pseudopalatus mccauleyi* (PEFO 31207; Parker & Irmis 2004) (most other *Pseudopalatus* specimens probably *P. buceros/P. pristinus*)
5. specimen of *Hesperosuchus agilis* (UCMP 129740; Parrish, 1991; Long & Murry 1995)
6. specimen of *Coelophysis* (UCMP 129618; Padian 1986)
7. specimen of *Chindesaurus bryansmalli* (PEFO 4849; Long & Murry 1995)
8. specimens of "coelophysoids" (e.g PEFO 33981), and *Chindesaurus bryansmalli*, including holotype (PEFO 10395; Long & Murry 1995) and other specimens (PEFO 33982; Parker & Irmis 2005)
9. holotype of *Kraterokheirodon colberti* (PEFO 9984, Irmis & Parker 2005)

Figure 6 Composite lithostratigraphic section for the Chinle Formation in Petrified Forest National Park showing the biostratigraphic ranges of tetrapod taxa. Ranges known within the park are shown in dark grey, while range extensions based on specimens from the Chinle Formation in other parts of Arizona and New Mexico are shown in light grey. Dicynodontia, Silesauridae, Shuvosauridae and Ravisuchide all extend into Middle Triassic strata (e.g. Nesbitt 2005b; Nesbitt *et al.* 2010), and paratypothoracisin aetosaurs and large metoposaurs are known from the Bluewater Creek Formation in New Mexico (Heckert 1997), which is probably equivalent to the Mesa Redondo Member (Stewart *et al.* 1972). The *Placerias* Quarry occurrence of coelophysoid' theropods (e.g. Nesbitt *et al.* 2007) and the Blue Hills occurrence of *Kraterokheirodon* (Irmis & Parker 2005) extend both into the Blue Mesa Member. The occurrence of silesaurids at the Hayden Quarry and Snyder Quarry in the Petrified Forest Member of New Mexico (Irmis *et al.* 2007b; Nesbitt *et al.* 2007) indicate that they also extend at least into the lower Revueltian. *Pseudopalatus*, *Typothorax*, *Trilophosaurus* and large metoposaurs are known from the Owl Rock Member at Ward's Terrace (Kirby 1991; Spielmann *et al.* 2007a). *Vancleavea campi*, Rauisuchidae and Shuvosauridae are known from the *Coelophysis* Quarry in the siltstone member of New Mexico (e.g. Long & Murry 1995; Nesbitt 2007; Nesbitt *et al.* 2007, 2009a), extending the range of all above that of the PEFO section. As the higher taxa Rauisuchidae and Shuvosauridae have ranges which extend completely through the PEFO section (from the Middle Triassic to the top of the Chinle Formation), they are completely biostratigraphically uninformative within PEFO, although they are included.

ornamentation consisting entirely of pitting and lacking elongate grooves (Long & Ballew 1985; Long & Murry 1995; Heckert & Lucas 2000; Martz 2002). Lucas *et al.* (2002) described another species, *Typothorax antiquum* (Fig. 7c), which they argued could be distinguished from *T. coccinarum* by having narrower paramedian osteoderms (width/length ratios 2–3), ornamentation that was 'coarser and less dense' and 'shallower' (Lucas *et al.* 2002, p. 222), and also based on differences in the ornamentation of the lateral osteoderms. Lucas *et al.* (2002) claimed that *T. antiquum* was restricted to the Adamanian, whereas *T. coccinarum* was restricted to the Revueltian. Lucas *et al.*'s (2002) description of a 'coarser and
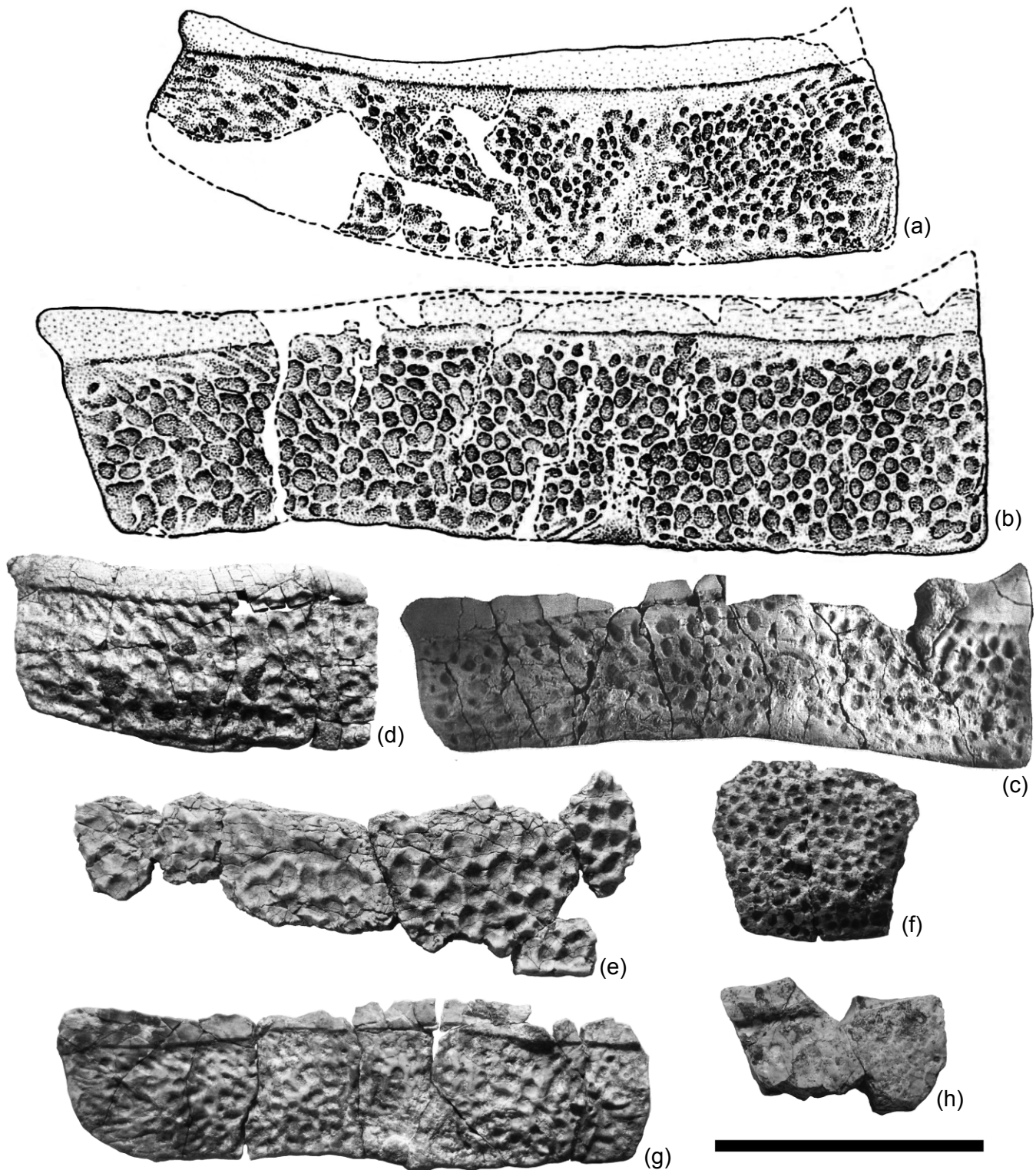
Figure 7 *Typothorax* and indeterminate aetosaur paramedian osteoderms from the Sonsela Member of Petrified Forest National Park in dorsal view: (a) UCMP V2816/34227, anterior dorsal osteoderm; (b) UCMP V2816/34227, posterior dorsal osteoderms [reversed]; (c) NMMNH P-36075, holotype of *Typothorax antiquum* from the (NMMNHS locality 3108) lower(?) Dockum Group of eastern New Mexico (modified from Lucas *et al.* 2002, fig. 3); (d) PEFO 34918 from the Kellogg Butte sandstones in Saurian Valley (PFV 097); (e) PEFO 4879 from the upper Jim Camp Wash beds in Hell Wash (PFV 037); (f) PEFO 5039 also from Hell Wash; (g) PEFO 33980 from the Giving Site (PFV 231) in the Petrified Forest Member of Petrified Forest National Park; (h) PEFO 26694 from the uppermost Blue Mesa Member or Camp Butte beds of Phytosaur Basin (PFV 121). Scale bar = 10 cm.

less dense' ornamentation is interpreted as meaning that there are fewer shallow pits per plate in *T. antiquum* than in *T. coccinarum*, and that in *T. antiquum* the pits are separated from each other by broader flat surfaces, rather than the narrower ridges in *T. coccinarum* (compare Fig. 7c with Fig. 7a–b).

Within PEFO, *Typothorax* paramedian osteoderms are extremely common throughout the Sonsela and Petrified Forest Members. Recovered osteoderms are mostly incomplete, but identifiable by their combination of ornamentation, consisting entirely of non-radial pitting, raised anterior bars and thick

ventral struts. Lucas *et al.* (2002, p. 230) noted that they had "not examined the Sonsela osteoderms in detail and cannot ascertain to which species of *Typothorax* they pertain". However, the same authors later stated (Hunt *et al.* 2005a, p. 360) that "we believe that all these specimens (from the Sonsela Member) pertain to *Typothorax antiquum*", while identifying specimens from the Petrified Forest Member (their 'Painted Desert Member') as *T. coccinarum*. No explanation was provided for this assignment. The present authors therefore carefully examined all *Typothorax* osteoderms from the park that are available for study to try to establish whether osteoderm morphotypes can be distinguished using the criteria of Lucas *et al.* (2002) that also show stratigraphic separation. Because lateral osteoderms of *Typothorax* are rare from the Sonsela Member, the following discussion focuses on paramedian osteoderms, which are much more common.

It is not possible to distinguish all of the *Typothorax* osteoderms from both the Sonsela and Petrified Forest Members in PEFO from the extensive and undisputed material of *Typothorax coccinarum*, such as that collected from the Canjilon Quarry in the Petrified Forest Member of New Mexico (Fig. 7a–b; Long & Murry 1995; Martz 2002). This includes the stratigraphically lowest *Typothorax* osteoderm known from the park, PEFO 34918, from the Sonsela Member in Devil's Playground (Fig. 7d). This specimen possesses a distinct anterior bar, ventral strut and a random patterning of pits that does not appear any coarser and less dense than that in the Canjilon Quarry osteoderms.

Based on examination, variation is found in the size and shape of the pitting among *Typothorax* osteoderms, with some paramedian osteoderms having finer and more circular pits, whereas most have larger and more irregularly shaped pits. However, incomplete osteoderms with both pitting types co-occur stratigraphically, for example at the Hell Wash locality (PFV 037) in the upper part of the Sonsela Member (Fig. 7e–f). Moreover, both fine and coarse pitting normally occur in osteoderms in different regions of the carapace of a single individual, even within the same osteoderm, where the finest pitting usually occurs at the centre of ossification, and the coarsest occurs medial to it (Martz 2002). For the reasons given above and discussed previously by Parker (2006), the present authors remain unconvinced regarding the morphological or stratigraphic distinctiveness of *Typothorax coccinarum* and *T. antiquum*, and in any case, no specimens from PEFO can be recognised as distinct from *T. coccinarum* and pertaining to *T. antiquum* (e.g. Fig. 7d–g).

Parker & Irmis (2005, fig. 5e) assigned an isolated fragment of aetosaur osteoderm (PEFO 26694; Fig. 7h) from Phytosaur Basin (PFV 121) to *Typothorax coccinarum*, and considered it to represent the lowest occurrence of that taxon in PEFO. Hunt *et al.* (2005a) considered this osteoderm to be indeterminate to species and the present authors concur with that assessment. Although the osteoderm is extremely thickened with the ventral strut typical for *Typothorax*, the surface ornamentation is too weathered to unequivocally assign the osteoderm to that taxon. Furthermore, some specimens of *Calyptosuchus*, *Adamanasuchus*, and *Paratypothorax* also possess thickened ventral struts (Martz 2002; Martz & Small 2006; Lucas *et al.* 2007b).

Parker (2006) followed Hunt (1998) in referring an aetosaur skeleton from the top of the Blue Mesa Member to *Typothorax*; however, Lucas *et al.* (2007b) referred this specimen to a new taxon, *Adamanasuchus eisenhardtae*. The present authors agree with the assessment that this specimen is a distinct taxon not referable to *Typothorax*. *Adamanasuchus* is also considered to be an aetosaurine that is similar to *Calyptosuchus*, and not a typothoracisine, based on the morphology of its lateral

osteoderms (WGP pers. obs.), which displays a strong phylogenetic signal within aetosaurs (Parker 2007). These referrals remove all of the *Typothorax* occurrences from the Blue Mesa Member and the base of the Sonsela Member mentioned by Parker (2006).

3.2. Other aetosaurs

Based on their own observations, the present authors agree with Harris *et al.* (2003) and Langer (2005) that *Calyptosuchus*, one of the most common Adamanian vertebrates in PEFO (Long & Ballew 1985), is probably not referable to *Stagonolepis*, in contrast with Heckert & Lucas (2000, 2002b). *Calyptosuchus wellesi* was assigned by Murry & Long (1989) to *Stagonolepis* with no explanation, but presumably because the paramedian osteoderms possess a radial pattern of grooves and ridges, as well as a dorsal eminence that contacts the posterior plate margin. This combination of characters is also found in *Aetosauroides scagliai* and *Stagonolepis robertsoni*, which was the basis for the synonymy of these taxa with *C. wellesi* by Heckert & Lucas (2000, 2002b). However, this character combination is plesiomorphic for aetosaurines (Parker 2007) and also found in some paratypothoracisins (e.g. *Paratypothorax*) and in *Neoaetosauroides engaeus* (Desojo & Báez 2005), which has never been referred to *Stagonolepis*. Moreover, *Calyptosuchus* also possesses many differences with *Aetosauroides* and *S. robertsoni* making the synonymy of these taxa ambiguous (Harris *et al.* 2003; Desojo 2004; Langer 2005; WGP unpublished data). Therefore *Calyptosuchus wellesi* is retained as a taxon distinct from *S. robertsoni* (*contra* Heckert & Lucas 2000, 2002b).

Aetosaurs of the clade Paratypothoracisini (Parker 2007) are common in the Sonsela Member, with the genera *Paratypothorax*, *Rioarribasuchus* and a *Tecovasuchus*-like form occurring within PEFO (Irmis 2005, p. 78). All paratypothoracisins share distinctive character combinations of the lateral and anterior paramedian osteoderms (Parker 2007). Therefore, isolated and incomplete osteoderms cannot usually be assigned to a specific genus (Martz & Small 2006; Parker 2007). Paratypothoracisin occurrences are plotted as a composite range for the taxon Paratypothoracisini, although it is noted that this range is composed partly from stratigraphic occurrences of specimens identifiable to particular genera (Fig. 4).

3.3. Phytosaurs

The phytosaur squamosal morphotype used to define and diagnose the Adamanian lvf was assigned to the genera *Rutiodon* (Ballew, 1989), *Leptosuchus*, and/or *Smilosuchus* in most recent studies (Long & Murry 1995; Irmis 2005; Parker & Irmis 2005). This squamosal morphotype differs from that of both basal phytosaurs and the derived taxon *Pseudopalatus* (e.g. Ballew 1989; Long & Murry 1995; Parker & Irmis 2006). Given that phytosaur squamosals are robust and frequently preserved as isolated elements, they provide an important source of biostratigraphic data.

However, recent work by Stocker (2008, 2010) indicates that *Rutiodon* is restricted to material from the Newark Supergroup of eastern North America, and that '*Leptosuchus*' (*sensu* Long & Murry 1995) probably constitutes a paraphyletic grade. Stocker's (2008, 2010) analysis placed *Machaeroprosopus adamanensis* and *Machaeroprosopus lithodendrorum* (both '*Leptosuchus*'-like taxa from the park with nearly complete skulls as holotypes; Camp 1930) within an unnamed clade that is distinct from the clade containing true *Leptosuchus* specimens (including the holotype for the genus; Case 1922) from the Dockum Group of Texas. However, members of both clades have the same squamosal morphotype (Parker & Irmis

2005, pp. 140–141), clearly identifiable and distinct from pseudopalatine squamosals. As most of the '*Leptosuchus*' specimens from PEFO consist of isolated squamosals, it is therefore uncertain whether true *Leptosuchus* might have also occurred in PEFO. Specimens from the park here referred to '*Leptosuchus*' therefore may represent a paraphylum.

The present authors recognise that some workers consider the use of paraphyletic taxa for biostratigraphy to be problematic on the grounds that they do not represent 'real' entities (e.g. Angielczyk & Kurkin 2003); however, the sharp distinction in the biostratigraphic distribution of the '*Leptosuchus*' squamosal morphotype from that of *Pseudopalatus* is difficult to ignore or dismiss as 'not real'. Thus, for the purposes of this study all phytosaur specimens in the park with this squamosal morphology are referred to '*Leptosuchus*'.

3.4. Metoposaurs

Large metoposaurs found within Upper Triassic strata in western North America have been traditionally assigned to *Koskinonodon* (*Buettneria*) *perfectum* or *Metoposaurus bakeri*, and small specimens to *Apachesaurus gregorii* (e.g. Hunt 1993; Long & Murry 1995), even when specimens are too incomplete to determine if they possess diagnostic characters of particular alpha taxa described by Hunt (1993). Virtually no skulls from the park expose the sutures around the orbital rim well enough to ascertain whether or not the lacrimal contacts the orbit, which is one of the only characters used to distinguish *Metoposaurus* from *Koskinonodon* (Hunt 1993; Sulej 2002, 2007; Milner & Schoch 2004).

Moreover, Sulej (2002, 2007) and Milner & Schoch (2004, pp. 246–247) introduced additional complications into North American metoposaur taxonomy by re-evaluating which characters are shared between various European and North American taxa. The taxonomic significance of the lacrimal character is unclear, so that it is difficult to be certain which North American specimens should be assigned to the European taxon *Metoposaurus*. We therefore refrain from assigning large metoposaurs to particular alpha taxa.

Most small metoposaur specimens from the park have not been adequately diagnosed to establish if they are adults of *Apachesaurus* or juveniles of larger taxa (Irmis 2005). We currently refrain from assigning specimens to *Apachesaurus* unless they clearly possess the elongate centra diagnostic of that taxon (Hunt 1993; Milner 1994). Other small metoposaur specimens are considered Metoposauridae *incertae sedis*, and are not considered biostratigraphically informative.

4. The stratigraphic position of vertebrate localities and their diagnostic specimens

Five members of the Chinle Formation are recognised in PEFO; from oldest to youngest these are the Mesa Redondo, Blue Mesa, Sonsela, Petrified Forest and Owl Rock Members (Figs 4–6). This lithostratigraphic model and nomenclature mostly follows Woody (2006) and Parker (2006), who modified the older models of Cooley (1957), Roadifer (1966), Stewart *et al.* (1972), Billingsley (1985), Ash (1987), Murry (1990), Lucas (1993) and Heckert & Lucas (2002a). The stratigraphic limits of the Blue Mesa Member and Sonsela Member also follow Woody (2006) and in part Heckert & Lucas (2002a), with the internal lithostratigraphy of the Sonsela Member in both the northern and southern parts of the park following published (Martz & Parker 2010) and ongoing revisions. The Petrified Forest Member (*sensu* Woody 2006) is equivalent to the unit referred to by previous workers as the upper Petrified Forest Member (e.g. Roadifer 1966; Billingsley 1985; Ash

1987; Murry 1990) and Painted Desert Member (Lucas 1993; Heckert & Lucas 2002a). Bed-level correlations for the Sonsela and Petrified Forest Members between the northern and southern part of the park are based on ongoing revisions.

The Mesa Redondo Member, Blue Mesa Member, Sonsela Member and the lower part of the Petrified Forest Member are exposed in the southern part of PEFO, whereas the Sonsela Member, Petrified Forest Member and Owl Rock Member are exposed in the northern part of PEFO. Vertebrate fossils have only recently been recovered from the Owl Rock Member inside the park, although Kirby (1989, 1991) and Spielmann *et al.* (2007a) described fossils from the Owl Rock Member of northern Arizona outside the park. Vertebrate fossils are completely unknown from the Mesa Redondo Member.

4.1. Central and southern PEFO

4.1.1 Blue Mesa Member. No vertebrate localities are currently known from the lower part of the Blue Mesa Member. The Newspaper Rock Bed, a lithologically complex marker bed in the middle of the Blue Mesa Member (e.g. Stagner 1941; Ash 1974; Parker 2006), is rich in trace and plant fossils, the latter including the majority of the non-woody plant fossils from the park (Daugherty 1941; Demko 1995; Ash 2001). Biostratigraphically significant plant fossils from this horizon (localities PFP 001, PFP 002, PFP 004, PFP 017, PFP 018, PFP 022), include the fern *Todites fragilis* (e.g. UCMP 1539), the fern-like foliage *Marcouia neuropteroides* (e.g. USNM 172279) and *Cladophlebis daughertyi* (e.g. PEFO 810), the benittitalean *Zamites powelli* (e.g. PEFO 1031) and the enigmatic *Dinophyton spinosus* (e.g. PEFO 31359) (Ash 2005; Parker 2006). These taxa are characteristic of the *Dinophyton* floral zone (Ash 1980). Litwin *et al.* (1991) listed a palynomorph assemblage (samples R4339 and R4342) assignable to their Palynomorph Zone II from this horizon.

The stratigraphically lowest vertebrate fossil occurrences in the Chinle Formation in PEFO, from just outside the traditional (pre-2004) park boundary and inside the new expansion area around Billings Gap (Fig. 2), are from within the top of the Newspaper Rock Bed (the red paleosol facies of Parker 2006). These include a '*Leptosuchus*' skull (TMM 43685–261) from locality PFV 339 and a partial skeleton of *Poposaurus gracilis* (TMM 43683–1) from locality PFV 336 (Weinbaum & Hungerbühler 2007). Osteoderms of *Adamanasuchus* (PEFO 35093), a crocodylomorph ilium (PEFO 35118), and a probable theropod dinosaur femur (PEFO 35117) have also been recovered from above the Newspaper Rock Bed in this area (PFV 337). This would be the lowest occurrence of a dinosaur in the park. Other sites within 10 metres of the top of the Newspaper Rock Bed in the Tepees area (Fig. 2) include PFV 111, PFV 112, PFV 142, PFV 182 and PFV 198, which produced *Calyptosuchus* (UCMP V82273/126854), '*Leptosuchus*' (PEFO 31156), *Desmatosuchus spurensis* (PEFO 31177) and crocodylomorphs (PEFO 26681), as well as small (PEFO 26679) and large metoposaurs (UCMP V7041/84744, Parker & Irmis 2005). Petrified wood and compression fossils of plants are present in this interval, but less common than in facies of the Newspaper Rock Bed. A bluish mudstone horizon a few metres above the Newspaper Rock Bed contains numerous specimens of *Dinophyton spinosus* (PFP 025, USNM 43648). In this same horizon is a concentration of more than forty upright conifer stumps (PFP 066, Gottesfeld 1972; Ash & Creber 1992), some of which show signs of fire damage (Jones & Ash 2006).

Two intervals near the top of the Blue Mesa Member around Blue Mesa (Fig. 2), a lower greenish grey siltstone and an upper dark purple mudstone immediately below the base of the Sonsela Member, contain several of the most rich and

diverse vertebrate fossil localities in the park (Camp 1930; Long & Murry 1995), including the Dying Grounds (PFV 122) and Crocodile Hill (PFV 124; Murry & Long 1989; Long & Murry 1995; Heckert 2004; Parker 2005a). These beds represent the type locality of the Adamanian land vertebrate faunachron (Lucas & Hunt 1993). Vertebrate fossils from these horizons include the holotype of '*Leptosuchus*' *adamanensis* (UCMP 7038/26699), the aetosaurs *Calyptosuchus wellesi* (PEFO 26667) and *Desmatosuchus spurensis* (e.g. PEFO 26668), the possible procolophonid *Colognathus* (UCMP V7038/136075; see Irmis 2005: fig. 4C–D), the holotype of the archosauriform *Vancleavea campi* (PEFO 2427) and the enigmatic tetrapod *Acallosuchus rectori* (UCMP V7038/27096; Long & Murry 1995; Heckert 2004; Hunt *et al.* 2005b; Irmis 2005; Parker & Barton 2008). Large metoposaur material (e.g. UCMP V7038/26695), is extremely common in this unit. Rarer tetrapod taxa include the archosauriform *Crosbysaurus harrisae* (PEFO 20336), a dicynodont (UCMP 7038/27095), *Trilophosaurus buettneri* (PEFO 3893) and the holotype of the aetosaur *Adamanasuchus eisenhardtae* (PEFO 34638; Murry 1989; Long and Murry 1995; Heckert 2004; Lucas *et al.* 2007b). This horizon also produced the proximal end of a femur of a non-dinosaurian dinosauriform similar to *Silesaurus* (PEFO 34347), the only known occurrence of a silesaurid (*sensu* Nesbitt *et al.* 2010) from the Chinle Formation of Arizona. (Parker *et al.* 2006; Nesbitt *et al.* 2007). Locality PFV 053, which produced a skull of *Pseudopalatus pristinus*, (AMNH 7222) was hypothesised to lie within the Blue Mesa Member based on historical photographs (Stocker 2008); however, this locality was recently physically relocated, and actually lies much higher in section within the Jim Camp Wash beds of the Sonsela Member.

4.1.2. Sonsela Member. The basalmost unit of the Sonsela Member, the Camp Butte beds (Martz & Parker 2010), is highly fossiliferous where exposed at the base of Blue Mesa. There they contain '*Leptosuchus*' (e.g. PEFO 34921), *Calyptosuchus* (UCMP V82249/126844), *Vancleavea campi* (PEFO 34912), large metoposaurs (e.g. PEFO 4833) and the stratigraphically lowest paratypothoracisin aetosaurs recovered from the park (e.g. PEFO 34632). *Poposaurus gracilis* (PEFO 34865) and 'rauisuchid' material probably referable to *Postosuchus* (PEFO 34044) also occur in this horizon together at locality PFV 161 near Agate Mesa (Fig. 2), the highest known occurrence of *Poposaurus* in the Chinle Formation. As already discussed, the aetosaur osteoderm (PEFO 26694) from Phytosaur Basin (PFV 121) previously referred to *Typothorax coccinarum* (Parker & Irmis 2005) is an indeterminate aetosaurine. An archosauromorph similar to *Trilophosaurus* or *Malerisaurus* (PEFO 31174) also occurs at PFV 161 (B. Mueller pers. comm. 2004).

Because of poor exposures, outcrops of the overlying Lot's Wife beds (Martz & Parker 2010) were not as thoroughly prospected as other units, and thus few specimens are known from this unit. The most prominent locality, Battleship NW (PFV169), occurs in the upper Lot's Wife beds west of Crystal Forest (Fig. 2) and produced a fairly complete skeleton of *Calyptosuchus wellesi* (PEFO 31217), a paratypothoracisin aetosaur (PEFO 34825) and the skull (PEFO 34034) of a new taxon of '*Leptosuchus*' (Parker & Irmis 2005; Stocker 2008, 2010). Other taxa from the Lot's Wife beds include large metoposaurs (WGP pers. obs.), an indeterminate crocodylomorph (PEFO 31164), and the holotype specimen of *Trilophosaurus dornorum* (PEFO 31165), which represents the highest occurrence of *Trilophosaurus* in the park (Parker & Irmis 2005; Mueller & Parker 2006).

The unit in the park exposed north of the Flattops (Fig. 2) traditionally called the Sonsela Sandstone bed (now the Jasper Forest bed; Raucci *et al.* 2006; Martz & Parker 2010), is considered to be correlative with the Rainbow Forest Bed exposed south of the Flattops (*contra* Cooley 1957; Roadifer 1966; Billingsley 1985; Ash & Creber 1992; Heckert & Lucas 1998a, 2002a; Woody 2006). This interval therefore contains the all the major concentrations of conifer log 'forests' in the southern part of the park (Crystal Forest, Jasper Forest and Rainbow Forest; Fig. 2) with reddish and multicoloured wood preserved through replacement (Ash 2005, p. 54). These logs were traditionally referred to *Araucarioxylon arizonicum* (Ash & Creber 2000; Ash 2005), which Savidge (2007) recently determined to be restricted to the holotype (as *Pullisilvaxylon arizonicum*) from the Black Forest Bed (Petrified Forest Member; see below). Recent work has assigned various single fossil conifer specimens from the Jasper Forest bed to new taxa such as *Arboramosa semicircumtrachea* Savidge & Ash, 2006, *Protocupressinoxylon arizonica* Savidge, 2006, *Silicisilvaxylon imprimicrystallus* Savidge, 2007, *Silicisilvaxylon secundacrystallus* Savidge, 2007 and *Crystalloxylon imprimicrystallus* Savidge, 2007. Palynomorph samples R4340 and R4341 (Litwin *et al.* 1991), which contain a Pollen Zone II assemblage, are from the tops of the Jasper Forest and Rainbow Forest beds.

Hunt *et al.* (2002) claimed that the Jasper Forest bed, although rich in petrified wood, was nearly devoid of vertebrate fossils; however, important vertebrate localities occur in localised friable sandstone facies of the Jasper Forest bed (Martz & Parker 2010). The most notable site is PFV 173 (Crystal Forest Buttes) just east of Crystal Forest (Fig. 2), which produced much of a carapace of the aetosaur *Paratypothorax* (PEFO 3004; Long & Ballew 1985; Hunt & Lucas 1992; Lucas *et al.* 2006). Although Hunt & Lucas (1992) and Lucas *et al.* (2006) assigned PEFO 3004 to *Paratypothorax andressorum*, Long & Murry (1995) considered it to be a distinct taxon, and its taxonomic affinities are currently being reevaluated. A '*Leptosuchus*' squamosal (UCMP V82238/126988) is also known from this locality (PFV 173) and a poorly preserved portion of a phytosaur skull (UCMP A257/27149) from the slightly higher Cowboy Site (PFV 154) is probably also '*Leptosuchus*' (R. Irmis pers. comm. 2005; *contra* Camp 1930). This site also yielded a large metoposaur (PEFO 31192). Vertebrates recovered from the finer-grained upper portion of the Rainbow Forest Bed include a partial '*Leptosuchus*' skull (PEFO 34866), and osteoderms of a paratypothoracisin aetosaur (PEFO 26706). Material of a large metoposaur was also recognised but not collected (WGP pers. obs.). This occurrence (PEFO 34866) of '*Leptosuchus*' is the stratigraphically highest in the Chinle Formation at PEFO.

The Jim Camp Wash beds, which overlie the Jasper Forest bed and Rainbow Forest Bed, are the best exposed and most intensely sampled interval in the member. The base of the Jim Camp Wash beds produced the aetosaur *Calyptosuchus* including a well-preserved partial carapace (PEFO 34045), from the Milkshake Quarry (PFV 304) southeast of Rainbow Forest (Fig. 2), just a few metres above the base of the Jim Camp Wash beds. This is the highest occurrence of *Calyptosuchus* in the park. Several metres above the base of the Jim Camp Wash beds is a narrow interval containing layers of densely packed silicified roots and woody material (the persistent red silcrete zone; Ash & Creber 1992; Creber & Ash 1992; Woody 2006; Martz & Parker 2010).

Immediately above the persistent red silcrete zone, the Jim Camp Wash beds provide a characteristic Revueltian (Lucas & Hunt 1993) fauna with abundant specimens of *Typothorax coccinarum*, *Paratypothorax* (e.g. PEFO 31206, PEFO 34565, PEFO 34631) and *Pseudopalatus pristinus* (e.g. PEFO 34042; AMNH 7222) known from numerous localities, especially those north of Rainbow Forest near Mountain Lion Mesa

(Fig. 2). AMNH 7222, a skull collected by E. H. Colbert in 1946 in Billings Gap at PFV 053, and PEFO 34042, a partial skull from north of Rainbow Forest at PFV 210, represent the lowest occurrences of *Pseudopalatus* from the park. Rarer constituents include a fragmentary 'rauisuchid' femur (PEFO 31183) from PFV 210, and the holotype of *Pseudopalatus jablonskiae* Parker & Irmis, 2006 (PEFO 31207) from locality PFV 295 at Mountain Lion Mesa (Fig. 2). Small metoposaurids, including partial skulls (e.g. PEFO 31184) and a clavicle (PEFO 23332), are known from several sites (PFV 089, PFV 210, PFV 272, PFV 253); however, only locality PFV 272 preserves the characteristic elongate vertebrae often assigned to *Apachesaurus gregorii* (PEFO 26705). The proximal femur of a theropod dinosaur (PEFO 31187) was recovered from locality PFV 089 (Parker & Irmis 2005, fig. 7i–j). Localised lacustrine deposits produce compression fossils of *Equisetites* (PFP 126) and *Zamites powelli* (PFP 107) (WGP pers. obs.; Herrick *et al*. 1999), both common in the *Dinophyton* floral zone of Ash (1980).

The Martha's Butte beds (Martz & Parker 2010) represent the uppermost portion of the Sonsela Member and are bracketed by several discontinuous ledge-forming Flattops One sandstones (= the 'Camp Wash Zone' of Roadifer 1966). These beds are well exposed northeast of Rainbow Forest and north of the Flattops around Martha's Butte and Mountain Lion Mesa (Fig. 2). *Typothorax* and *Pseudopalatus* are the most common vertebrates in this interval, with *Typothorax* known from PFV 060 (CFMNH/PR 1562), PFV 075 (e.g. UCMP V82240/126926), PFV 092 (PEFO 34214), and PFV 349 (PEFO 34848). *Pseudopalatus* is known from PFV 092 (PEFO 4860), PFV 271 (PEFO 31205), and PFV 354 (PEFO 34612). The holotype specimen of *P. mccauleyi* Ballew, 1989 (UCMP V82040/126999) is from PFV 055, which is low in the Martha's Butte beds at Billings Gap. 'Rauisuchid' material similar to *Postosuchus* (PFV 055/PEFO 4851) is also present from this locality (Long & Murry 1995). The paratypothoracisin aetosaurs *Paratypothorax* (e.g. UCMP 82240/126912) and *Rioarribasuchus* (e.g. UCMP 82240/129829, PFV 075/PEFO 31162; Parker & Irmis 2005, fig. 4f) are also found in the Martha's Butte beds, with *Paratypothorax* the more common form. The Walker's Stump plant locality (PFP 006) situated below Martha's Butte (Fig. 2) in one of the Flattops One sandstones at the base of the Martha's Butte beds produces material of *Pagiophyllum simpsoni* (e.g. USNM 43621), *Zamites powelli* and *Dinophyton spinosus* (e.g. USNM 43655). This is the highest occurrence of these taxa and thus represents the top of the *Dinophyton* floral zone in the park. Palynomorph sample R4359 (Litwin *et al*. 1991) from the same locality represents a Pollen Zone III assemblage.

4.1.3. Petrified Forest Member. The uppermost exposures of the Chinle Formation in the southern portion of PEFO comprise the Petrified Forest Member (*sensu* Woody 2006;= the Painted Desert Member *sensu* Lucas 1993; Heckert & Lucas 2002a= the upper Petrified Forest Member of most previous workers; e.g. Cooley 1957; Roadifer 1966; Billingsley 1985; Ash 1987; Murry 1990). At the southern end of PEFO, this member is mainly restricted to the Flattops region and on Mountain Lion Mesa (Fig. 2). Three prominent sandstone ledges in this area were named the Flattops Beds 2–4 (Billingsley 1985; Heckert & Lucas 2002a). The surface just above Flattops Bed 2 is locally fossiliferous. Sites at this level (PFV 070 and PFV 071) produced specimens of *Typothorax* (PEFO 23388) and *Paratypothorax* (UCMP V82259/126958), as well as an indeterminate phytosaur (PEFO 23347) and theropod (UCMP V82259/126751).

Palynomorph sample R4347 (Litwin *et al*. 1991) is also from above Flattops Bed 2 and represents a Pollen Zone III

assemblage. Vertebrate fossil localities are unknown from above the Flattops Bed 3, but Litwin (1986) documents a palynomorph sample (PFDN40) from this level that contains a Pollen Zone III assemblage.

4.2. Northern PEFO
4.2.1. Sonsela Member. Based upon data collected from our ongoing stratigraphic revisions, the Sonsela Member is the most basal member of the Chinle Formation exposed in the northern end of the park (*contra* Billingsley 1985; Lucas 1993; Steiner & Lucas 2000; Heckert & Lucas 2002a), specifically in the Devil's Playground area and at the base of The Citadel (Fig. 2). In these areas, the Sonsela Member consists of a stacked sequence of fluvial deposits, including eight prominent sandstone-dominated units, for which both published (Billingsley 1985) and unpublished (R. Long unpublished notes 1981–1985) names were used. From lowest to highest, these are the Fossil Garden sandstone, Kellogg Butte sandstones (a heterolithic package of ledge- and slope-forming sandstones, conglomerates, and mudstones), lower Brown sandstone, upper Brown sandstone (Billingsley 1985), Ledge sandstone, Goblin sandstone, Little Eagle's Nest sandstones (another heterolithic interval containing ledge-forming sandstones which cap the section in Devil's Playground) and Painted Desert sandstone one (Billingsley 1985), which is considered to form the top of the Sonsela Member.

Correlations between these beds and beds in the Sonsela Member in the southern part of PEFO are based on a similar pattern of facies changes within the member. The Fossil Garden sandstone is hypothesised to be equivalent to part of the Lot's Wife beds, based on correlations of sandstones higher in the section. The stratigraphically higher Kellogg Butte sandstones contains abundant reddish and multicoloured petrified wood, and are correlated with the Jasper Forest bed. The Brown sandstone of Billingsley (1985) is actually two sandstone beds, which locally both have a distinctive dark brown colour and an unusual weathering pattern. Several workers have correlated the upper Brown sandstone to the Jasper Forest bed (Camp 1930; Murry 1990; Parker 2006; and possibly Ash & Creber 1992), but current investigations suggest that it, and the lower Brown sandstone, lie slightly higher, in the lower part of the Jim Camp Wash beds. Immediately above the Brown sandstones, pedogenic carbonate nodules become extremely abundant, both in mudstones and conglomerates, as they do in the Jim Camp Wash beds in the southern PEFO (Martz & Parker 2010); the Ledge and Goblin sandstones lay within this interval. Finally, the Little Eagle's Nest sandstones and Painted Desert sandstone one are yellowish compositionally and texturally immature sandstones similar to the Flattops One sandstones in the Martha's Butte beds of southern PEFO. The transition to the purple and reddish mudstone-dominated beds of the Petrified Forest Member occurs immediately above these sandstones, as it does also in southern PEFO (Martz & Parker 2010).

Several fossil localities in the Fossil Garden sandstone, such as PFV 098 (Fossil Garden) and PFV 097 (Saurian Valley), produced numerous phytosaur skulls (e.g. UCMP 7034/27181a; Camp 1930) including the type specimen of '*Machaeroprosopus*' *lithodendrorum* (=*Leptosuchus crosbiensis sensu* Long & Murry 1995; UCMP 7034/26688). Camp & Welles (1956, p. 256) also reported postcranial elements (UCMP 7034/26682) of a *Placerias*-like dicynodont from this horizon. A partial skeleton of the aetosaur *Calyptosuchus* (PEFO 34919) recently was recovered from the Fossil Garden sandstone at PFV 224 and represents the highest occurrence of this taxon in the northern part of the park. Other taxa include a large metoposaur (UCMP 7034/129998), a 'rauisuchian'

(UCMP 7034/40171), and a paratypothoracisin aetosaur (UCMP 7034/129995).

The Kellogg Butte sandstones also contain fossil vertebrates such as a large metoposaur skull (PFV 100/ PEFO 4843) and skulls of *Pravusuchus hertus* (e.g. PFV 099/ PEFO 31218, PFV 100/ PEFO 34239) sharing some characters (e.g. a subsidiary opisthotic process of the squamosal) with *Pseudopalatus* (Stocker 2008, 2010). A partial paramedian osteoderm (PFV 367/ PEFO 34918) probably referable to *Typothorax coccinarum* was discussed earlier, and represents the lowest occurrence of the taxon in PEFO. The Kellogg Butte sandstones also contain a fossil plant locality (PFP 049) that produced *Dinophyton spinosus* (PEFO 17512) and a Pollen Zone II assemblage (Litwin & Ash 1991).

PFV 325 is from the top of the upper Brown sandstone (probably in the lower Jim Camp Wash beds) and has produced vertebrate fossils, mostly phytosaur teeth and scutes, archosaurian vertebrae and osteoderm fragments assignable to *Typothorax* (WGP pers. obs.). PFV 039 occurs a few metres above the top of the upper Brown sandstone and has produced the lowest occurrence of *Pseudopalatus* (e.g. PEFO 5080) in the northern part of the park, as well as osteoderms referable to *Paratypothorax* (PEFO 4898).

The Lost Backpack locality (PFV 371) lies between the Ledge and Goblin sandstones in the Jim Camp Wash beds, and has produced osteoderms of *Typothorax* (e.g. PEFO 35131) and *Paratypothorax* (PEFO 35133). Several localities occur just above the Goblin sandstone. *Pseudopalatus* (PEFO 5034) and *Typothorax* (PEFO 5032) were collected from PFV 037, as was the highest definite specimen of *Paratypothorax* (PEFO 34177). Small metoposaurs (PEFO 34190; PEFO 34292) also occur just above the Goblin sandstone at PFV 037. Plant fossils (PFP 120) are also present at this level, including pollen sample R4394, which produced a Zone III palynoflora (S. Ash, pers. comm. 2009).

Vertebrate specimens have recently been recovered from the lower Little Eagle's Nest sandstones in Devil's Playground by workers from the Los Angeles Natural History Museum (localities PFV 373, 374, 375). These include an osteoderm of *Typothorax* and an indeterminate paratypothoracisin, as well as an unprepared phytosaur skull (JWM pers. obs.). No localities are known from higher in the Martha's Butte beds in northern PEFO, and the next highest localities are over 60 metres higher in the section, well within the Petrified Forest Member (Fig. 5).

4.2.2. Petrified Forest Member. The mudstone-dominated strata of the Petrified Forest Member are immediately above Painted Desert sandstone one. Although these mudstones are predominantly reddish, the base of the member is locally more than ten metres of purple mudstone; this is also seen at the base of the Petrified Forest Member in the southern part of the park (the 'monotonous purple beds' of Martz & Parker 2010). Above this are several discontinuous sandstones occurring at different stratigraphic levels, the 'Painted Desert two sandstones' (Billingsley 1985; Johns 1988). Capping this interval is a prominent ledge-forming sandstone, capping mesas and cliffs along much of Lithodendron Wash, that Billingsley (1985) called Painted Desert sandstone three, and Heckert and Lucas (2002a) renamed the Lithodendron Wash Bed. On the basis of the stratigraphic distance of these sandstones above the top of the Sonsela Member, one or more of the 'Painted Desert two sandstones' are considered to be roughly correlative with the Flattops Two and Three Beds, and the Lithodendron Wash Bed to be roughly correlative with the Flattops Four Bed (unpublished data). Numerous discontinuous sandstone lenses occur between the Lithodendron Wash Bed and the Black Forest Bed, which are referred to as the Painted Desert four sandstones after Johns (1988).

No vertebrate fossils localities are currently known from the lower part of the Petrified Forest Member below the Lithodendron Wash Bed in the northern part of the park. However, the top of the Lithodendron Wash Bed, some of the Painted Desert four sandstones, and the interval in between, are highly fossiliferous. Many of the vertebrate fossil localities from the north end of the park and mainly southwest of Painted Desert Mesa (Fig. 2) are found at these horizons, including Dinosaur Hollow, Billingsley Hill, the Giving Site and the *Revueltosaurus* Quarry (Therrien & Fastovsky 2000; Parker et al. 2005; Parker & Irmis 2005). Dinosaur Hollow (PFV 020) is the type locality of the basal theropod *Chindesaurus bryansmalli* (PEFO 10395, Long & Murry 1995; Therrien & Fastovsky 2000). It has been determined that, because of mapping errors by Billingsley (1985), some workers (e.g. Long & Murry 1995; Therrien & Fastovsky 2000; Parker 2006) erroneously placed many of these localities (and the Dinosaur Hill locality, see below) below the Lithodendron Wash Bed.

The Giving Site (PFV 231) is the most taxonomically diverse locality in the Petrified Forest Member of PEFO. Taxa present at this locality include *Revueltosaurus callenderi* (PEFO 33991), *Typothorax coccinarum* (PEFO 33967), *Pseudopalatus* (PEFO 33990), *Vancleavea campi* (PEFO 33978), a 'rauisuchid' similar to *Postosuchus* (PEFO 33954), a shuvosaurid (PEFO 33953) and *Apachesaurus gregorii* (PEFO 33977). This site also provided specimens of a crocodylomorph (PEFO 34087). The Giving Site is significant because it is the richest dinosaur-bearing site in the Chinle Formation of Arizona, containing several individuals of a theropod similar to *Coelophysis* (e.g. PEFO 33981) and a specimen of *Chindesaurus* (PEFO 33982). The nearby *Revueltosaurus* Quarry (PFV 297) is a few metres above the level of the Giving Site and contains numerous specimens of the pseudosuchian *Revueltosaurus callenderi* (e.g. PEFO 33787) and a shuvosaurid (e.g. PEFO 33920; Parker et al. 2005).

The holotype of the enigmatic tooth taxon *Kraterokheirodon colberti* (PEFO 9984) was collected from just above the Lithodendron Wash Bed at the Billingsley Hill locality (PFV 034). The only other known specimen of this taxon (AMNH 4947) is known from basal Chinle Formation outcrops northeast of St Johns, Arizona (Irmis & Parker 2005).

PFV 018 is situated between the Lithodendron Wash Bed and a Painted Desert four sandstone. This locality contains *Chindesaurus bryansmalli* (PEFO 4849) and an indeterminate theropod (Long & Murry 1995). The Petroglyph phytosaur locality (PFV 042) is also in the reddish mudstones in this same interval. This site produced a well-preserved, fully crested phytosaur skull and associated postcrania that Long & Murry (1995) assigned to *Pseudopalatus buceros*, but was referred to *P. mccauleyi* by Parker & Irmis (2004).

Two vertebrate localities, Dinosaur Hill (PFV 040) and Zuni Well Mound (PFV 215), are situated within Painted Desert four sandstones. The Dinosaur Hill locality was previously considered stratigraphically lower than Painted Desert sandstone two (Therrien & Fastovsky 2000), just below the Lithodendron Wash bed (Parker 2006), or just above it (Heckert & Lucas 2002a), but recent detailed mapping by the present authors (unpublished data) shows it to be stratigraphically higher. The Dinosaur Hill assemblage is well studied (e.g. Padian 1986, 1990; Murry & Long 1989; Parrish 1991; Long & Murry 1995; Hunt & Wright 1999) and includes *Revueltosaurus callenderi* (PEFO 34169), *Vancleavea campi* (PEFO 34170), *Hesperosuchus* (UCMP V82250/129740), *Apachesaurus gregorii* (UCMP V82250/129900), *Typothorax coccinarum* (UCMP V82250/126952), *Pseudopalatus* (UCMP V82250/

126983) and a theropod dinosaur (UCMP V82250/129618) tentatively referred to *Coelophysis bauri* (Padian 1986; Spielmann *et al.* 2007c), but which may represent a new taxon (Hunt *et al.* 1996, 1998b; Hunt & Wright 1999). Taxa from Zuni Well Mound (PFV 215) include an indeterminate phytosaur (PEFO 34879), *Typothorax coccinarum* (PEFO 16668), *Vancleavea campi* (PEFO 34035), *Revueltosaurus callenderi* (PEFO 16671), *Apachesaurus gregorii* (PEFO 31170), an indeterminate dinosauriform (PEFO 34863), and a large metoposaur (PEFO 31173) (Hunt & Wright 1999; Parker & Irmis 2005; Parker & Barton 2008).

The next highest fossiliferous level is the Black Forest Bed, a reworked tuffaceous sandstone with a basal carbonate nodule conglomerate (Ash 1992; Riggs *et al.* 2003). The Black Forest Bed is important, because until recently it was the only bed in the Chinle Formation with published isotopic dates (213 ± 1.7 Ma, possibly as young as 209 Ma, Riggs *et al.* 2003; 211 ± 0.7 Ma, Heckert *et al.* 2009). Fossil specimens from the Black Forest Bed (mainly from locality PFV 002) include *Pseudopalatus* (e.g. UCMP V82241/126750), *Typothorax coccinarum* (e.g. UCMP V82241/126933), and *Postosuchus* (UCMP V82241/139499; Long & Murry 1995). *Typothorax coccinarum* (WGP pers. obs.) is known also from the basal conglomerate at PFV 299. The distal end of a large dinosauriform femur (PFV 184; PEFO 34562) was collected approximately from the Black Forest Bed horizon by Michael Parrish in 1988 (PEFO unpublished data).

Long & Murry (1995) listed *Paratypothorax* as present in the Black Forest Bed. This would represent the highest occurrence of *Paratypothorax* in the park and demonstrate a range extension for this taxon into the Petrified Forest Member. The voucher specimen used by Long & Murry (1995) for this assignment is PEFO 4866, a badly weathered and fragmented medial portion of a paramedian plate. The ornamentation is barely perceptible on this plate, but is radial unlike that seen in *Typothorax*. Therefore it probably represents a paratypothoracisin aetosaur, as paratypothoracisins (*Paratypothorax* and *Rioarribasuchus*) are the only aetosaurs with radial ornamentation known from the Revueltian, though this character is found in other non-paratypothoracisin aetosaurs.

Vertebrate localities above the Black Forest Bed in PEFO are rare. PFV 302 and PFV 269 are in a zone of discontinuous conglomerates called the Rabbit Foot Hill conglomerates that lie several metres above the Black Forest Bed and approximately ten metres below the Owl Rock Member (see below). These sites have produced a small metoposaurid (PEFO 19561), the aetosaur *Typothorax coccinarum* (PEFO 34929) and a shuvosaurid (PEFO 34924), a squamosal of *Pseudopalatus*, and other phytosaur material (WGP & JWM pers. obs.).

4.2.3. Owl Rock Member. Owl Rock Member outcrops in PEFO were described in detail by Dubiel (1993). Vertebrate fossils were unknown for this unit within PEFO until the discovery of the rostrum of a phytosaur (PEFO 34939) in the lower part of the member in 2009. It has also been recently determined that locality PFV 357 is immediately above a distinctive purple-grey paleosol that can be traced for many kilometres along the base of Chinde Mesa, a horizon that Dubiel (1993) placed as the base of the Owl Rock Member. The present authors concur with this stratigraphic assignment and note that it differs from the base of the Owl Rock determined by Ash (1992) and Lucas (1993) to lie at the base of the first limestone lens, a difference of approximately 40 metres. PFV 357, discovered from the purple-grey paleosol horizon in 2008, produced *Typothorax coccinarum* and other specimens currently under study by researchers at Yale University. Workers from Columbia College (Chicago) and

the Smithsonian have also recently recovered abundant microvertebrate material from higher in the Owl Rock Member, although most specimens are indeterminate tetrapods that are still under preparation and study. The Owl Rock Member is highly fossiliferous elsewhere in Arizona and contains a diverse fauna including *Pseudopalatus*, *Typothorax*, a shuvosaurid, *Trilophosaurus* and large metoposaurs (Kirby 1989, 1991; Spielmann *et al.* 2007a).

5. Discussion

5.1. The stratigraphic ranges of taxa in the Chinle Formation of Petrified Forest National Park and the location of the Adamanian/Revueltian boundary

When biostratigraphic data are plotted on the revised lithostratigraphy (Figs 4–6; Table 1), the biostratigraphic overlap between Adamanian and Revueltian biozones is virtually eliminated, because the ranges of nearly all index taxa alleged to be of the Adamanian and Revueltian are now distinct. The purported overlap between the Adamanian and Revueltian faunas (Woody & Parker 2004; Hunt *et al.* 2005a; Parker 2006) was the result of lithostratigraphic miscorrelation of the Flattops One sandstones with the Jasper Forest bed, and of the Jim Camp Wash beds with the Lot's Wife beds (Martz & Parker 2010). The Lot's Wife beds and Jasper Forest bed contain an Adamanian fauna, whereas the Jim Camp Wash beds and Flattops One sandstones contain a Revueltian fauna. Mistakenly correlating these units and, consequently the vertebrate localities they contain, created the illusion of a faunal overlap (e.g. Fig. 1b), even though characteristic Adamanian and Revueltian taxa do not actually co-occur at the same localities, as noted by Parker (2006). Moreover, the current revisions make it possible to narrow down the exact stratigraphic interval in which the overturn between characteristic Adamanian and Revueltian taxa occurred.

In the southern part of the park, this overturn occurred at the level of the persistent red silcrete zone in the lower Jim Camp Wash beds, not at the base of the slightly lower Jasper Forest bed as previously suggested (e.g. Long & Ballew 1985; Long & Padian 1986; Long & Murry 1995; Hunt & Lucas 1995a). The stratigraphic ranges of '*Leptosuchus*' and the aetosaur *Calyptosuchus*, both of which are considered Adamanian index fossils (e.g. Lucas & Hunt 1993; Lucas 1998), extend upwards to just a few metres below the persistent red silcrete zone. The ranges of the phytosaur *Pseudopalatus* and the aetosaur *Typothorax*, both of which are considered Revueltian index fossils, both extend down to immediately above the persistent red silcrete zone. Because the LSD (lowest known stratigraphic occurrence) of *Pseudopalatus* defines the base of the Revueltian (Lucas 1998), '*Leptosuchus*' and *Calyptosuchus* are currently unknown from the Revueltian (as they both occur below the LSD of *Pseudopalatus*). There is therefore is no 'Lamyan' zone of overlap between the Adamanian index taxa and *Pseudopalatus*. As a result, the redefinition of the base of the Revueltian by Hunt *et al.* (2005a) using *Typothorax coccinarum*, which was done because of the alleged range overlap, is unnecessary as there is no distinct faunal assemblage that characterises this interval. Those four taxa have the most densely sampled stratigraphic ranges of any taxa in the park, and the lower Jim Camp Wash beds, where the transition occurs, is the most densely sampled stratigraphic interval (Fig. 4). This indicates that this abrupt transition may be a reality rather than an artifact of sampling bias.

In the northern part of the park, the stratigraphic interval in which the Adamanian–Revueltian transition occurs is less

Table 1 Voucher specimens used to construct stratigraphic range charts in Figures 4 and 5.

Taxon 1	Taxon 2	Locality #	Stratigraphic Unit	Voucher #
Phytosauria	Phytosauridae	PFV070	Petrified Forest Member (lower part)	PEFO 23347
		PFV215	Petrified Forest Member (lower part)	PEFO 34879
		PFV361	Owl Rock Member	PEFO 34939
	'Leptosuchus'	PFV113	upper Blue Mesa Member	UCMP 139554
		PFV123	upper Blue Mesa Member	UCMP 26699[1]
		PFV142	upper Blue Mesa Member	PEFO 31156
		PFV339	upper Blue Mesa Member	TMM 43684–8
		PFV339	upper Blue Mesa Member	TMM 43685–261
		PFV161	Camp Butte beds	PEFO 34921
		PFV097	Lot's Wife beds	UCMP 26688[10]
		PFV098	Lot's Wife beds	UCMP 27181a
		PFV169	Lot's Wife beds	PEFO 34034[5]
		PFV154	Jasper Forest bed	UCMP 27149
		PFV173	Jasper Forest bed	UCMP 126988
		PFV177	Rainbow Forest Bed	UCMP 129809
		PFV178	Rainbow Forest Bed	PEFO 34866
	Pravusuchus	PFV099	Kellogg Butte sandstone	PEFO 31218
		PFV100	Kellogg Butte sandstone	PEFO 34239
	Pseudopalatus	PFV053	Jim Camp Wash beds	AMNH 7222
		PFV037	Jim Camp Wash beds	PEFO 5034
		PFV039	Jim Camp Wash beds	PEFO 5080
		PFV210	Jim Camp Wash beds	PEFO 34042
		PFV227	Jim Camp Wash beds	PEFO 34628
		PFV290	Jim Camp Wash beds	PEFO 34855
		PFV295	Jim Camp Wash beds	PEFO 31207[7]
		PFV055	Martha's Butte beds	UCMP 126999[8]
		PFV092	Martha's Butte beds	PEFO 4860
		PFV271	Martha's Butte beds	PEFO 31205
		PFV354	Martha's Butte beds	PEFO 34612
		PFV040	Petrified Forest Member (lower part)	PEFO 126983
		PFV042	Petrified Forest Member (lower part)	PEFO 31219
		PFV231	Petrified Forest Member (lower part)	PEFO 33990
		PFV002	Black Forest Bed	UCMP 126750
Archosauria	Revueltosaurus callenderi	PFV040	Petrified Forest Member (lower part)	PEFO 34169
		PFV215	Petrified Forest Member (lower part)	PEFO 16671
		PFV231	Petrified Forest Member (lower part)	PEFO 33991
		PFV297	Petrified Forest Member (lower part)	PEFO 33787
Aetosauria	Calyptosuchus	PFV111	upper Blue Mesa Member	UCMP 126854
		PFV112	upper Blue Mesa Member	UCMP 126856
		PFV212	upper Blue Mesa Member	PEFO 26667
		PFV162	Camp Butte beds	UCMP 126844
		PFV288	Camp Butte beds	PEFO 31175
		PFV 165	Lot's Wife beds	UCMP 126943
		PFV167	Lot's Wife beds	PEFO 34191
		PFV169	Lot's Wife beds	PEFO 31217
		PFV224	Lot's Wife beds	PEFO 34919
		PFV355	Lot's Wife beds	PEFO 34616
		PFV304	Jim Camp Wash beds	PEFO 34045
	Typothorax	PFV367	Kellogg Butte sandstone	PEFO 34918
		PFV037	Jim Camp Wash beds	PEFO 5032
		PFV094	Jim Camp Wash beds	UCMP 126855
		PFV095	Jim Camp Wash beds	PEFO 31189
		PFV227	Jim Camp Wash beds	PEFO 34627
		PFV268	Jim Camp Wash beds	PEFO 26702
		PFV290	Jim Camp Wash beds	PEFO 34871
		PFV295	Jim Camp Wash beds	PEFO 34280
		PFV371	Jim Camp Wash beds	PEFO 35131
		PFV060	Martha's Butte beds	CFMNH PR1562
		PFV075	Martha's Butte beds	UCMP 126926
Aetosauria	Typothorax	PFV092	Martha's Butte beds	PEFO 34214
		PFV349	Martha's Butte beds	PEFO 34848

Table 1 *Continued.*

Taxon 1	Taxon 2	Locality #	Stratigraphic Unit	Voucher #
Aetosauria	*Typthorax*	PFV040	Petrified Forest Member (lower part)	UCMP 126952
		PFV070	Petrified Forest Member (lower part)	PEFO 23388
		PFV215	Petrified Forest Member (lower part)	PEFO 16668
		PFV231	Petrified Forest Member (lower part)	PEFO 33967
		PFV002	Black Forest Bed	UCMP 126933
		PFV302	Petrified Forest Member (upper part)	PEFO 34929
	Paratypothoracisini	PFV161	Camp Butte beds	PEFO 34632
		PFV097	Lot's Wife beds	UCMP 129995
		PFV169	Lot's Wife beds	PEFO 34825
		PFV173	Jasper Forest bed	PEFO 3004
		PFV259	Jasper Forest bed	PEFO 26690
		PFV178	Rainbow Forest Bed	PEFO 26706
		PFV037	Jim Camp Wash beds	PEFO 34177
		PFV039	Jim Camp Wash beds	PEFO 4898
		PFV087	Jim Camp Wash beds	PEFO 4892
		PFV089	Jim Camp Wash beds	PEFO 34565
		PFV089	Jim Camp Wash beds	PEFO 34631
		PFV095	Jim Camp Wash beds	PEFO 31145
		PFV177	Jim Camp Wash beds	PEFO 26706
		PFV272	Jim Camp Wash beds	PEFO 31206
		PFV268	Jim Camp Wash beds	PEFO 26701
		PFV290	Jim Camp Wash beds	PEFO 34856
		PFV307	Jim Camp Wash beds	PEFO 31198
		PFV371	Jim Camp Wash beds	PEFO 35133
		PFV075	Martha's Butte beds	UCMP 126912
		PFV075	Martha's Butte beds	UCMP 129829[9]
		PFV075	Martha's Butte beds	PEFO 31162[9]
		PFV092	Martha's Butte beds	PEFO 34887
		PFV002	Black Forest Bed	PEFO 4866*
	Desmatosuchus spurensis	PFV198	upper Blue Mesa	PEFO 31177
		PFV202	upper Blue Mesa	PEFO 23338
		PFV212	upper Blue Mesa	PEFO 26668
	Acaenasuchus	PFV211	upper Blue Mesa	PEFO 16621
	Adamanasuchus	PFV339	upper Blue Mesa Member	PEFO 35093
		PFV263	upper Blue Mesa Member	PEFO 34638[4]
Paracrocodylomorpha	Rauisuchidae	PFV161	Camp Butte beds	PEFO 34044
		PFV096	Lot's Wife beds	UCMP 40171
		PFV210	Jim Camp Wash beds	PEFO 31183
		PFV055	Martha's Butte beds	PEFO 4851
		PFV231	Petrified Forest Member (lower part)	PEFO 33954
		PFV002	Black Forest Bed	UCMP 139499
	Poposaurus	PFV336	lower Blue Mesa Member	TMM 43683–1
		PFV161	Camp Butte beds	PEFO 34865
	Shuvosauridae	PFV231	Petrified Forest Member (lower part)	PEFO 33953
		PFV297	Petrified Forest Member (lower part)	PEFO 33920
		PFV302	Petrified Forest Member (upper part)	PEFO 34924
	'Sphenosuchia'	PFV198	upper Blue Mesa Member	PEFO 26681
		PFV211	upper Blue Mesa Member	PEFO 16662
		PFV339	upper Blue Mesa Member	PEFO 35118
		PFV191	Lot's Wife beds	PEFO 31164
		PFV040	Petrified Forest Member (lower part)	UCMP 129740
		PFV231	Petrified Forest Member (lower part)	PEFO 34087
Archosauriformes	*Crosbysaurus*	PFV122	upper Blue Mesa Member	PEFO 20336
	Vancleavea	PFV121?	upper Blue Mesa Member	PEFO 24272
		PFV121	Camp Butte beds	PEFO 34912
		PFV040	Petrified Forest Member (lower part)	PEFO 34170
		PFV215	Petrified Forest Member (lower part)	PEFO 34035
		PFV231	Petrified Forest Member (lower part)	PEFO 33978
	Trilophosaurus	PFV122	upper Blue Mesa Member	PEFO 3893
		PFV191	Lot's Wife beds	PEFO 31165[6]
	cf. *Malerisaurus*	PFV161	Camp Butte beds	PEFO 31174

Table 1 *Continued.*

Taxon 1	Taxon 2	Locality #	Stratigraphic Unit	Voucher #
Archosauriformes	*Acallosuchus*	PFV124	upper Blue Mesa Member	UCMP 27096[3]
Ornithodira	Dinosauriformes	PFV 215	Petrified Forest Member (lower part)	PEFO 34863
		PFV002	Black Forest Bed	PEFO 34562
	Silesauridae	PFV122	upper Blue Mesa Member	PEFO 34347
	Theropoda	PFV339	upper Blue Mesa Member	PEFO 35117*
		PFV089	Jim Camp Wash beds	PEFO 31187
		PFV040	Petrified Forest Member	UCMP 129618
		PFV071	Petrified Forest Member (lower part)	UCMP 126751
		PFV231	Petrified Forest Member (lower part)	PEFO 33981
	Chindesaurus	PFV018	Petrified Forest Member (lower part)	PEFO 4849
		PFV020	Petrified Forest Member (lower part)	PEFO 10395[11]
		PFV231	Petrified Forest Member (lower part)	PEFO 33982
Synapsida	Dicynodontia	PFV113	Petrified Forest Member (lower part)	UCMP 139463
		PFV124	upper Blue Mesa Member	UCMP 27095
		PFV 098	Lot's Wife beds	UCMP 26682
incertae sedis	*Colognathus*	PFV124	upper Blue Mesa Member	UCMP 136075
	Kraterokheirodon	PFV034	Petrified Forest Member (lower part)	PEFO 9984
Metoposauridae	large forms	PFV111	upper Blue Mesa Member	UCMP 130020
		PFV112	upper Blue Mesa Member	UCMP 130022
		PFV142	upper Blue Mesa Member	UCMP 84744
		PFV124	upper Blue Mesa Member	UCMP 26695
		PFV199	upper Blue Mesa Member	PEFO 34287
		PFV205	upper Blue Mesa Member	PEFO 23384
		PFV121	Camp Butte beds	PEFO 4833
		PFV098	Lot's Wife beds	PEFO 129998
		PFV165	Lot's Wife beds	UCMP 129873
		PFV154	Jasper Forest bed	PEFO 31192
		PFV100	Kellogg Butte sandstone	PEFO 4843
		PFV215	Petrified Forest Member (lower part)	PEFO 31173
	small forms	PFV142	upper Blue Mesa Member	PEFO 26679
		PFV037	Jim Camp Wash beds	PEFO 34190
		PFV037	Jim Camp Wash beds	PEFO 34292
		PFV089	Jim Camp Wash beds	PEFO 23332
		PFV210	Jim Camp Wash beds	PEFO 31184
		PFV353	Jim Camp Wash beds	PEFO 35142
		PFV269	Petrified Forest Member (upper part)	PEFO 19561
	Apachesaurus	PFV211	upper Blue Mesa Member	PEFO 16663
		PFV272	Jim Camp Wash beds	PEFO 26705
		PFV040	Petrified Forest Member (lower part)	UCMP 129900
		PFV215	Petrified Forest Member (lower part)	PEFO 31170
		PFV231	Petrified Forest Member (lower part)	PEFO 33977

*Probable occurrence

[1] Holotype of *Smilosuchus adamanensis* (Camp 1930)

[2] Holotype of *Vancleavea campi* Long & Murry 1995

[3] Holotype of *Acallosuchus rectori* Long & Murry 1995

[4] Holotype of *Adamanasuchus eisenhardtae* Lucas *et al.* 2007b

[5] Possible new taxon according to Stocker (2008, 2010)

[6] Holotype of *Trilophosaurus dornorum* Mueller & Parker 2006

[7] Holotype of *Pseudopalatus jablonskiae* Parker & Irmis 2006

[8] Holotype of *Pseudopalatus mccauleyi* Ballew 1989

[9] Specimen assignable to *Rioarribasuchus chamaensis* (Parker 2007)

[10] Holotype specimen of *Smilosuchus lithodendrorum* (Camp 1930)

[11] Holotype specimen of *Chindesaurus bryansmalli* Long & Murry 1995

densely sampled (Fig. 5), so the biostratigraphic data are more ambiguous. However, the transition occurs somewhere between the Kellogg Butte sandstones and a few metres above the upper Brown sandstone, which are thought, on the basis of lithology, to be equivalent to the Jasper Forest bed and lowermost Jim Camp Wash beds respectively. The lowest known occurrence of *Pseudopalatus* is between the upper Brown sandstone and the Ledge sandstone, the highest known

Calyptosuchus occurrence at the top of the Fossil Garden sandstone, and the highest '*Leptosuchus*' in the Kellogg Butte sandstone (Fig. 5). It is interesting, and possibly evolutionarily significant, that all of the specimens of '*Leptosuchus*' in the Kellogg Butte sandstone, which are interpreted as occurring stratigraphically higher than other '*Leptosuchus*' specimens, are referable to a new taxon showing transitional character states between some taxa previously assigned to '*Leptosuchus*'

and pseudopalatines (Stocker 2008, 2010). This taxon is currently unknown from the southern end of the park.

Unlike in the southern part of the park, where the lowest known occurrence of *Typothorax* is equivalent to that of *Pseudopalatus* (Fig. 4) the lowest *Typothorax* specimen in the northern part of the park co-occurs with '*Leptosuchus*' in the Kellogg Butte sandstone (Fig. 5). The stratigraphic co-occurrence of *Typothorax* with Adamanian taxa was previously documented in the Dockum Group of eastern New Mexico and west Texas (Long & Murry 1995; Lehman & Chatterjee 2005; Martz 2008). Nonetheless, no evidence is found for two stratigraphically distinct species of *Typothorax* in PEFO, and the present authors do not overlap the range of *Typothorax* with those of Adamanian taxa as extensively as indicated by Hunt *et al.* (2005a, fig. 5). In both PEFO, and in west Texas (Martz 2008), the only places where the biostratigraphic ranges of taxa have been plotted in detail on a detailed and testable lithostratigraphic framework, the range of *Typothorax* does not extend far below the base of the Revueltian. *Typothorax* remains at best extremely scarce in the latest Adamanian, while being overwhelmingly the most abundant aetosaur in the Revueltian.

Lucas *et al.*'s (2002) assignment of the type specimen of *Typothorax antiquum* to the Adamanian was not based on its co-occurrence with Adamanian taxa at the same locality, but because of their identification of its alleged stratigraphic position as the Tres Lagunas Member of the Santa Rosa Formation. Despite a paucity of fossils, this unit is purportedly Adamanian in age, based presumably on superpositional relationship to strata producing Adamanian vertebrates (see Hunt & Lucas 1993a). Unfortunately much confusion exists regarding the placement of fossil localities in strata assigned to the upper part of the Santa Rosa Formation in east-central New Mexico (see Hunt & Lucas 1995b) as well as the identification of fossils recovered from these unit and the overlying Garita Creek Formation (e.g. Hunt & Lucas 1993a, b). Moreover, although some workers (Hunt & Lucas 1993a; Lucas *et al.* 2002; Hunt *et al.* 2005a) have considered the Tres Lagunas Member and the Garita Creek Formation to be Adamanian in age, others (e.g. Hunt & Lucas 1995b) considered these units to be Revueltian. Because of the ambiguity surrounding specimen identification from these units, because of Hunt & Lucas's (2005a) identification of *Pseudopalatus* (a Revueltian index taxon) from the same locality as *T. antiquum*, and also because the argument by Hunt *et al.* (2005a) for the occurrence of both *Pseudopalatus* and *Typothorax* in the lower Adamanian of PEFO was based on erroneous lithostratigraphic correlations (Martz & Parker 2010), we are sceptical of claims for an extensive overlap of *Typothorax* and *Pseudopalatus* with Adamanian taxa in the Santa Rosa Formation in eastern New Mexico, until the co-occurrence of Adamanian and Revueltian index taxa from the same locality can be unambiguously demonstrated.

The data seem to indicate a decline in aetosaur diversity throughout the Chinle Formation within PEFO. The most diverse known aetosaur fauna is in the Adamanian uppermost Blue Mesa Member, where *Calyptosuchus*, *Desmatosuchus spurensis*, *Acaenasuchus* and *Adamanasuchus* co-occur. Specimens from the *Placerias* Quarry demonstrate that paratypothoracisins were also present in this interval (Parker 2005a); however, only *Calyptosuchus* and paratypothoracisins are documented in the uppermost Adamanian of the lower Sonsela Member, whereas only *Typothorax* and paratypothoracisins occur in the lowermost Revueltian in the upper Sonsela Member. Furthermore, *Typothorax* is the only aetosaur documented with certainty through most of the Petrified Forest

Member in PEFO and in the Owl Rock Member on the Navajo Nation to the north (Kirby 1991).

Thus, paratypothoracisins are rare within the Blue Mesa Member, but extremely common throughout Sonsela Member deposition, before disappearing somewhere in the Petrified Forest Member. Paratypothoracisins referable to *Paratypothorax* or a *Tecovasuchus*-like taxon (Irmis 2005) are present through most of the Sonsela Member, but the few specimens from the park referable with certainty to *Rioarribasuchus* ('*Desmatosuchus*' *chamaensis*; Irmis 2005, p. 75) are known only from the lower Revueltian Martha's Butte beds at the top of the member. Although a possible badly preserved paratypothoracisin plate is known from the Black Forest Bed, paratypothoracisins are unknown from the stratigraphically lower and extremely rich interval just above the Lithodendron Wash Bed, suggesting that the Black Forest Bed occurrence may be reworked. Aside from the Black Forest Bed, the highest definite paratypothoracisin specimen is from near the base of the Petrified Forest Member (Fig. 4).

Several taxa seem to be almost entirely restricted to the Adamanian. *Trilophosaurus* specimens from PEFO are restricted entirely to pre-Revueltian strata. Martz (2008) revised lithostratigraphic correlations in the Dockum Group of West Texas and showed that all *Trilophosaurus* occurrences there are probably Adamanian/Otischalkian (*contra* Spielmann *et al.* 2007b). The *Trilophosaurus* tooth from the Owl Rock Member described by Kirby (1991) is the only known post-Adamanian occurrence of the taxon, and its validity has been questioned (Spielmann *et al.* 2007b). The poposauroid 'rauisuchian' *Poposaurus* is also known only from pre-Revueltian occurrences (Long & Murry 1995; Lucas 1998; Weinbaum & Hungerbühler 2007).

The possibility that the aetosaur *Desmatosuchus smalli* also crossed the Adamanian–Revueltian boundary is based on a single occurrence from the Martha's Butte beds that was documented by Long & Ballew (1985) and Parker (2005b). This occurrence consists of a fragment of a lateral plate with a morphology more consistent with *D. smalli* than with *D. spurensis* (Parker 2005b, fig. 4). The provenance of this specimen is not entirely certain (see Long & Ballew 1985 p. 59), but if this information and the taxonomic assignment are correct, it represents the only occurrence of *D. smalli* in the Chinle Formation (Parker 2005b) as well as a range extension for that taxon, because the type locality, the Post Quarry, of *D. smalli* in the Cooper Canyon Formation (Dockum Group) of Texas is Adamanian in age (Martz 2008).

As noted by previous workers (Camp 1930; Long & Padian 1986; Hunt & Lucas 1993b; Irmis 2005) large metoposaurs are far more common in the Adamanian than in the Revueltian. Their remains are extremely abundant in the upper Blue Mesa Member and are often found in the lower part of the Sonsela Member. However, the only known large metoposaur occurrences above the LSD of *Pseudopalatus* are known from an interclavicle (PEFO 35139) from above the Lithodendron Wash Bed at PFV 376 and from a single centrum (PEFO 31173) from above the Painted Desert four sandstones at Zuni Well Mound (PFV 015), high in the Petrified Forest Member. These finds, in combination with Kirby's (1991) description of fragmentary specimens in the Owl Rock Member at Ward's Terrace, indicate that large metoposaurs were present, although extremely rare, during the Revueltian. In contrast, *Apachesaurus* is much more common in the Revueltian than in the Adamanian (Hunt & Lucas 1993b).

Other taxa are known from material too fragmentary to establish exactly how alpha taxonomy was impacted by the Adamanian–Revueltian transition, if at all. The basal archosauriform *Vancleavea*, and remains of large 'rauisuchids', are

both known from the Adamanian Blue Mesa Member in the *Placerias* Quarry to the Apachean siltstone member at the top of the Chinle Formation in New Mexico (Long & Murry 1995; Hunt *et al*. 2005b; Weinbaum 2007; Parker & Barton 2008; Nesbitt *et al*. 2009a), although only a part of these stratigraphic ranges are recorded in PEFO. Although both Adamanian and Revueltian 'rauisuchid' material from PEFO compares favourably to more complete Adamanian specimens of *Postosuchus kirkpatricki* (Long & Murry 1995; Weinbaum 2007), the park specimens are mostly isolated elements, and referral to either the genus or species is ambiguous. Given the long stratigraphic range of both *Vancleavea* and 'rauisuchids', it seems doubtful that alpha taxonomy remained stable for these taxa for the entire interval.

Shuvosaurids ('chatterjeeids') are known only from the middle of the Revueltian Petrified Forest Member in PEFO; however, their occurrence in the Apachean 'siltstone member' in New Mexico (Nesbitt & Stocker 2008), the Adamanian Post Quarry in Texas and *Placerias* Quarry in Arizona (Chatterjee 1993; Long & Murry 1995; Nesbitt 2007; Martz 2008), and the Early–Middle Triassic Moenkopi Formation in Arizona (Nesbitt 2005a), give Shuvosauridae a stratigraphic range longer than the total exposed Triassic section in PEFO. Although the Revueltian material from PEFO is too fragmentary to identify to an alpha taxon, the type locality of *Shuvosaurus inexpectatus* is Adamanian (Martz 2008) and that of *Effigia okeeffeae* is Apachean (Lucas *et al*. 2007c), indicating that evolution of the lineage was not static (Nesbitt 2007; Nesbitt & Norell 2006).

The pseudosuchian archosaur *Revueltosaurus callenderi* and the basal theropod *Chindesaurus bryansmalli* are both known only from a narrow stratigraphic interval in the Revueltian, between the Lithodendron Wash Bed and Painted Desert sandstone four in the Petrified Forest Member (Wright *et al*. 2001). Because there are extremely thick stratigraphic sections which are poorly sampled both below and above this interval, it is unclear how real this apparent stratigraphic restriction is. Nonetheless, the absence of these taxa in the densely sampled lower Revueltian Jim Camp Wash beds and Martha's Butte beds suggests the possibility that at least *Revueltosaurus callenderi* is truly absent in the lower Revueltian (although the range of *Chindesaurus* may extend into the Adamanian; see below). *Revueltosaurus* material is known from the Adamanian Blue Hills locality near St Johns, Arizona. This material (osteoderms and skull elements; e.g. UCMP V7308/165205) was found in association with teeth referred to a second species of *Revueltosaurus*, *R. hunti* and current recognised specimens of this taxon from Arizona and New Mexico are restricted to the Adamanian (Heckert 2002).

Dinosaur remains are rare and generally fragmentary, and most can only be identified as theropod based on femur morphology (Parker & Irmis 2005; Nesbitt *et al*. 2007). The basal theropod *Chindesaurus* (Nesbitt *et al*. 2009c) co-occurs with a coelophysoid theropod in the Petrified Forest Member between the Lithodendron Wash Bed and Painted Desert sandstone four. Moreover, coelophysoid material is known from the Adamanian *Placerias* Quarry (Hunt *et al*. 1998b; Nesbitt *et al*. 2007), which is probably almost as old as any localities in PEFO (see discussion below), and a partial femur from *Chindesaurus* (or a closely related form) is known from the Otis Chalk Quarries in the Dockum Group of Texas (Long & Murry 1995; Nesbitt *et al*. 2007, pp. 228–229) which are pre-Revueltian (Lucas 1998; Martz 2008). These occurrences indicate that basal neotheropods and more basal carnivorous dinosaurs (herrerasaurians) co-existed throughout most of Chinle deposition (Irmis *et al*. 2007b).

The presence of a *Silesaurus*-like basal dinosauriform (Nesbitt *et al*. 2007) and the dinosauromorph *Dromomeron gregorii* (also from the *Placerias* Quarry; see Nesbitt *et al*. 2009b) in the Blue Mesa Member is evidence for at least four types of dinosauromorphs (lagerpetids, silesaurids, herrerasaurians and basal neotheropods/coelophysoids) co-existing in the Adamanian (Parker *et al*. 2006; also see Nesbitt & Chatterjee 2008). All four groups are also present in the Revueltian Hayden Quarry of New Mexico (Irmis *et al*. 2007b; Nesbitt *et al*. 2009c). Unfortunately, although overall dinosauromorph diversity may not have changed across the Adamanian–Revueltian boundary (Fig. 3), most dinosauromorph material is too taxonomically indeterminate to evaluate whether the Adamanian–Revueltian transition is reflected in dinosauriform alpha taxonomy. The possible exception is the Adamanian *Placerias* Quarry species *Dromomeron gregorii*, which is distinct from the Revueltian *D. romeri* (Irmis *et al*. 2007b; Nesbitt *et al*. 2009b).

The *Placerias* Quarry is located in the St Johns area south of PEFO, and is famous for its diverse vertebrate fauna, which is nearly identical to that of the Adamanian Blue Mesa Member fauna in PEFO (e.g. Long & Murry 1995; Lucas & Heckert 1996b). Based on our ongoing investigations into the stratigraphy of the St Johns and PEFO areas, we suggest that the *Placerias* Quarry lies within the Blue Mesa Member ('lower Petrified Forest Member') as previously hypothesised (Camp & Welles 1956; Jacobs & Murry 1980; Murry & Long 1989; Kaye & Padian 1994; Long & Murry 1995). This is in contrast to Lucas & Heckert (1996b) and Lucas *et al*. (1997), who claimed that the *Placerias* Quarry lies near the base of the stratigraphically lower Bluewater Creek Member. Because the vertebrate specimens from the Bluewater Creek Member and correlative Monitor Butte Member are mostly taxonomically undiagnostic (e.g. Parrish & Good 1987; Heckert 1997) the placement of the *Placerias* Quarry in the Blue Mesa Member nearly eliminates our knowledge of taxonomic diversity in the lowermost Chinle Formation, and indicates that the stratigraphically lowest localities in PEFO are among the lowest known to produce specimens diagnostic to alpha taxon.

5.2. Implications for the Tr-4 unconformity

Lucas (1991, 1993) argued for the presence of a large basin-wide unconformity (termed the Tr-4) representing an extended period of lowstand erosion, separating the Adamanian and Revueltian faunal assemblages in the southwestern United States, and also approximating the Carnian–Norian boundary. In PEFO, this unconformity was placed initially at the base of the Jasper Forest bed, which was hypothesised by several workers (e.g. Long & Ballew 1985; Hunt & Lucas 1995a) to be the boundary of the tetrapod faunal overturn and a possible floral change (e.g. Litwin *et al*. 1991). The apparently abrupt biotic reorganisation was one important piece of evidence presented that this unconformity represented an extended hiatus (Lucas 1991, 1993; Heckert & Lucas 1996). However, Herrick (1999) noted that the absence of a well-developed paleosol below the base of the Jasper Forest bed argued against the existence of an extended hiatus. Additionally, deposition of most or all of the Chinle Formation, including the Sonsela Member, is now thought to be Norian (Irmis & Mundil 2008). The Tr-4 unconformity, even if it exists, would therefore not approximate the Carnian–Norian boundary.

At Jasper Forest and Agate Mesa, Heckert & Lucas (2002a) moved the location of the Tr-4 unconformity from the base of the Jasper Forest bed to the base of their expanded Sonsela Member (named the Camp Butte beds by Martz & Parker 2010) without any explanation. Subsequently, Hunt *et al*. (2005a) argued that the Adamanian–Revueltian transition was

gradual rather than abrupt, but did not discuss any implications for the existence of the Tr-4 unconformity. Woody (2006) and Martz & Parker (2010) noted that the base of the Sonsela Member and the top of the underlying Blue Mesa Member consisted of complexly interbedded sandstone lenses and mudstone, and was not a single erosional unconformity, whereas Martz (2008) noted that the same was true of the alleged position of the Tr-4 unconformity in western Texas. Moreover, recognition that much of the type section of the Blue Mesa Member (Lucas 1993) is now referable to the Mesa Redondo and Sonsela Members (Woody 2006; Lucas *et al.* 2007d; Martz & Parker 2010) significantly thins the Blue Mesa Member in PEFO. The thickness of the Blue Mesa Member in PEFO (∼50 metres, units 2–15 in Lucas' 1993 type section; Martz & Parker 2010, fig. 5b) is now roughly consistent with that of the Blue Mesa Member near Fort Wingate (45 metres, Heckert & Lucas 2002c), eliminating much of the erosional relief postulated by Heckert & Lucas (1996) as evidence for a major unconformity.

Plotting tetrapod biostratigraphic ranges using our revised lithostratigraphic model demonstrates that a faunal and floral reorganisation does occur, but at a level just above the Jasper Forest bed, rather than at its base as hypothesised previously (e.g. Long & Ballew 1985; Long & Padian 1986; Hunt & Lucas 1995a). The base of the Jasper Forest bed is a local unconformity near the middle of the Sonsela Member, but only one of numerous disconformities in the Sonsela and Petrified Forest Members (Kraus & Middleton 1987; Martz & Parker 2010). Because of this, and the lack of evidence for a biotic turnover at either of the levels where the Tr-4 unconformity was alleged to exist, the present authors follow Herrick (1999), Woody (2006) and Martz (2008) in doubting its existence as a basin-wide erosional hiatus comparable to the Tr-3 unconformity at the base of the Upper Triassic section (Pipiringos & O'Sullivan 1978).

5.3. The Adamanian–Revueltian turnover and the rise of dinosaurs

It must be borne in mind that the apparent stratigraphic ranges of taxa documented by the biased and highly incomplete fossil record are not a perfect reflection of the true ranges of the taxa (e.g. Marshall 1998; Walsh 1999; McKenna & Lillegraven 2006; Irmis *et al.* 2010). Apparent ranges can only be considered to approximate the true ranges of taxa with a large and stratigraphically dense sample size. If the fossil record for a taxon is relatively scanty, as it is for Triassic vertebrates, then a considerable margin of error must be applied to the apparent range (e.g. Marshall 1998). This becomes an especially important consideration when attempting to identify a mass extinction event, which requires determining whether or not multiple taxa disappeared simultaneously in a very narrow stratigraphic interval (Newell 1982; Signor & Lipps 1982; Dingus 1984; Springer 1990; Benton 1994a; Lucas 1994).

An interval in the Chinle Formation of PEFO, at which it is hypothesised that an abrupt faunal overturn might have taken place, occurs at the level of the persistent red silcrete (Martz & Parker 2010) in the southern part of the park, and possibly at about the level of the upper Brown sandstone in the northern part. 'Leptosuchus' and *Calyptosuchus* disappear at approximately this level, almost coinciding with the lowest occurrence of the phytosaur *Pseudopalatus* and a dramatic increase in the abundance of the aetosaur *Typothorax*. The highest known dicynodonts occur close to this level in the northern region of the park as well, and large metoposaurs are abundant below this level, although the latter continue to be encountered rarely in the Revueltian. Several other taxa (including *Trilophosaurus*, *Poposaurus* and *Desmatosuchus spurensis*) are only known

from well below the persistent red silcrete level, although so few specimens are known for these taxa that it is difficult to infer whether their true ranges might have approached it. Further intensive prospecting to increase the sample size is required to test whether these taxa truly disappeared, or at least suffered a major decrease in abundance, at the same stratigraphic level. Nonetheless, the possibility that the Adamanian–Revueltian turnover represents at least a localised mass extinction event for western North America is a tentative but plausible hypothesis (*contra* Lucas 1994).

Litwin *et al.* (1991) documented a palynomorph turnover (between Palynomorph Zones II and III) in the Chinle Formation, which in PEFO also occurs somewhere in the Jim Camp Wash beds. However, the turnover is not yet sufficiently well-constrained to determine if it occurred at the same level as the tetrapod turnover. In southern PEFO, the palynomorph turnover occurs somewhere between the Rainbow Forest Bed and Martha's Butte beds (Fig. 4), whereas in northern PEFO it lies somewhere between the top of the Kellogg Butte sandstones and the top of the Goblin sandstone (Fig. 5). Moreover, Murry (1990) and Murry & Kirby (2002) also noted a turnover in non-tetrapod vertebrate taxa at about the level of the Jasper Forest bed. It is possible therefore that the vertebrate faunas, as well as the flora, all experienced a roughly synchronous turnover midway through the deposition of the Sonsela Member. Interestingly, although the palynomorph record demonstrates a floral turnover in the Sonsela Member, the plant macrofossil record does not reflect this change. Taxa characteristic of Ash's (1980) *Dinophyton* floral zone (e.g. *Dinophyton spinosus*, *Zamites powelli*) occur from the top of the lower portion of the Blue Mesa Member (i.e. the Newspaper Rock Bed) to base of the Martha's Butte beds. However, this may simply be due to poor sampling throughout these intervals, because the majority of the non-petrified wood plant microfossils in the park are only known from the level of the Newspaper Rock Bed.

On the basis of vertebrate and pollen-based correlations to marine strata in Europe, both those floral and faunal turnovers were long thought to roughly coincide with the Carnian–Norian boundary (e.g. Litwin *et al.* 1991; Cornet 1993; Lucas 1998), which was thought to occur at about 216 Ma (e.g. Gradstein & Ogg 2004). However, using magnetostratigraphy, the Carnian–Norian boundary was recently re-approximated at about 228 Ma (Muttoni *et al.* 2004; Furin *et al.* 2006), and a date of about 219 Ma was recently acquired from the base of the Blue Mesa Member near Fort Wingate (Irmis & Mundil 2008), which correlates stratigraphically well below the turnover level at PEFO. These dates indicate that most of the Chinle Formation, including the interval of the Adamanian–Revueltian and Palynomorph Zone II–III turnovers, occurred well within the Norian (Irmis *et al.* 2010; *contra* Heckert *et al.* 2009). They therefore do not coincide with evidence of increased aridity, and turnovers in the marine invertebrate community, that occurred at the Carnian–Norian boundary (e.g. Simms *et al.* 1994) as postulated by Benton (1994b). Moreover, recent work by Muttoni *et al.* (2010) suggested that the Norian–Rhaetian boundary is about 207–210 Ma. Based on these data, dates for the Black Forest Bed of 211 ± 0·7 Ma (Heckert *et al.* 2009) or 213 ± 1·7 Ma (Riggs *et al.* 2003) suggest that the upper part of the Petrified Forest Member and the Owl Rock Member (and, therefore, the upper part of the Revueltian biozone) may be Rhaetian in age.

Sedimentological evidence indicates that the faunal and floral transition within the Chinle Formation coincided with an increase in aridity in western North America (e.g. Dubiel 1994; Dubiel & Hasiotis 2010) during the Norian. Pedogenic carbonate nodules, vertisols and oxidised mudstones are more

prevalent in the Petrified Forest Member than in the older Blue Mesa Member of Arizona and the Monitor Butte Member of Utah, suggesting the development of an increasingly arid climate with lower water tables, and this drying trend continued into the Owl Rock and Rock Point Members (e.g. Stewart *et al.* 1972; Dubiel *et al.* 1991; Dubiel 1994; Tanner 2003; Tanner & Lucas 2006; Prochnow *et al.* 2006; Dubiel & Hasiotis 2010).

Our own work in the Sonsela Member in PEFO has narrowed down the stratigraphic interval in which this trend seems to begin. Carbonate nodules begin to form extremely dense concentrations in mudstones of the lower Jim Camp Wash beds, immediately above the persistent red silcrete zone, in the southern part of the park (Martz & Parker 2010) and immediately above the upper Brown sandstone, also in the lower Jim Camp Wash beds, in the northern part of the park (JWM & WGP unpublished data). In both areas, this is accompanied by a dramatic increase in intrabasinal carbonate nodules in channel conglomerates as they incised these carbonate rich mudstones, and also by spectacular local abundances of unionid bivalves, which may have benefited from increasingly alkaline stream waters (Martz & Parker 2010).

This sudden increase in pedogenic carbonate occurs in the same stratigraphic interval as the possible faunal and floral turnovers. A sudden increase in aridity would explain the relative paucity of large metoposaur amphibians in the Revueltian compared to the Adamanian (e.g. Long & Padian 1986; Hunt & Lucas 1993b) as wetland habitats became scarcer. The predominance of *Apachesaurus* in the Revueltian was noted by Hunt (1993), who argued that the loss of the otic notch, a less developed lateral line system, and more robust postcrania in *Apachesaurus* suggested a more terrestrial lifestyle. These characteristics may have developed in response to regional drying trends. A sudden increase in aridity might also explain the decrease in body size in aetosaurs postulated by Heckert *et al.* (2009), and the general decrease in faunal diversity with the apparent loss of dicynodonts, *Trilophosaurus*, *Poposaurus* and multiple aetosaur taxa, as the result of increasingly strenuous environmental conditions.

Both within the park and elsewhere, the disappearance of these taxa is followed by the appearance of new taxa in the Revueltian (*Pseudopalatus*, *Rioarribasuchus*, *Revueltosaurus callenderi*, *Dromomeron romerii*; Irmis *et al.* 2007b) related to forms occurring in the Adamanian (*Leptosuchus*, *Paratypothorax*, *Revueltosaurus hunti*; Heckert 2002, *Dromomeron gregorii*; Nesbitt *et al.* 2009b; Fig. 3). A faunal replacement involving closely related taxa and accompanied by evidence of climatic change is suggestive of Vrba's (e.g. 1985, 2005) concept of a 'turnover pulse'. Although the evidence for 'turnover pulses' for Cenozoic mammals has been questioned (e.g. Behrensmeyer *et al.* 1997; Davis 2005), turnover pulses have been suggested for faunal overturns involving Cretaceous dinosaurs (e.g. Sampson 2009, pp. 247–248). Although the currently available biostratigraphic data are far too scarce to argue forcibly for the Adamanian–Revueltian turnover being a 'turnover pulse', it is presented as a tentative hypothesis to be subjected to additional testing.

As the climatic changes in western North America which may have produced this faunal change were driven by the northward movement of western North America into the mid-latitudes (e.g. Kent & Olsen 2008; Dubiel & Hasiotis 2010), the current results emphasise the importance of considering localised as well as global environmental and faunal changes during the Late Triassic. These data, combined with the high degree of faunal endemism across Pangea during the Late Triassic (e.g. Benton 1983; Ezcurra 2010), as well as the potentially diachronous distribution of various vertebrate groups (e.g. dinosauromorphs; Irmis *et al.* 2007b; Irmis & Mundil 2008; Nesbitt *et al.* 2009c), suggest that Late Triassic faunal change may have been heavily influenced by localised environmental conditions and events.

A second, more dramatic, event may also coincide with the Adamanian–Revueltian turnover. The Late Triassic Manicouagan impact crater in Quebec is one of the largest known impact craters on Earth and yielded a U–Pb date of about 215·5 Ma (Ramezani *et al.* 2005). Unpublished radioisotopic dates for the stratigraphic interval containing the Adamanian–Revueltian transition in PEFO compare favourably with the age of the Manicouagan impact (Dunlavey *et al.* 2009). A possible coincidence of the Manicouagan impact with the floral and faunal turnovers in western North America cannot be discounted at this time (Olsen *et al.* 2011 (this volume); *contra* Heckert *et al.* 2009).

As noted by Hunt & Lucas (2004), the Adamanian–Revueltian faunal turnover cannot currently be tied to the ascension of dinosaurs in western North America. Although, as already discussed, overall dinosauromorph diversity remained high across the Adamanian–Revueltian boundary, the diversity and size of true dinosaurs in North America throughout the Late Triassic was low compared to the Early Jurassic (Nesbitt *et al.* 2007; Irmis *et al.* 2007b). The recent recognition that prosauropods and ornithischians were probably absent in western North America until the latest Triassic or Early Jurassic (Parker *et al.* 2005; Irmis *et al.* 2007a, b; Nesbitt *et al.* 2007) indicates that, at least in North America, the disappearance of dicynodonts cannot be attributed to competition with herbivorous dinosaurs (as previously argued by Benton 1986; Crompton & Attridge 1986). As the last known dicynodonts in the Chinle Formation and Dockum Group are Adamanian in age, there was a considerable lag (encompassing the entire Revueltian and Apachean) between the disappearance of dicynodonts and the rise of ornithischians and prosauropods in western North America.

Moreover, carnivorous dinosauromorphs continued to be relatively rare, though diverse (Irmis *et al.* 2007b; Nesbitt *et al.* 2009c; Sues *et al.* 2010), components of the vertebrate fauna throughout the Revueltian and Apachean in western North America. Although some Revueltian 'coelophysoids' may have reached more than five metres in length (*Gojirasaurus quayi*, Carpenter 1997; Nesbitt *et al.* 2007), most Late Triassic theropods, including Apachean forms (e.g. *Coelophysis bauri*; e.g. Rinehart *et al.* 2009), were much smaller, and they continued to co-exist with large rauisuchids within the Apachean/Rhaetian siltstone member in New Mexico (Long & Murry 1995; Weinbaum 2007). The role of theropods as the sole large terrestrial carnivores did not begin in North America with the Adamanian/Revueltian transition. If the ascent of dinosaurs in western North America was truly an opportunistic takeover as argued by Benton (1986), they chose a later opportunity which post-dated both the initiation of climatic change in western North America and the Manicouagan bolide impact.

5.4. Accepting the limits of Late Triassic vertebrate biochronology for global correlation

Lucas (1990) recognised and advocated the need for provincial biochronologies which, once established and well-tested, could be integrated into regional and potentially global biochronologies. However, in practice, Late Triassic biochronology was never built on the kind of detailed biostratigraphic data required to make it rigorous and testable (Irmis *et al.* 2010). Moreover, despite the vast amount of literature by Lucas and colleagues proposing numerous regional and global correlations (e.g. Hunt & Lucas 1991; Lucas & Huber 1994; Heckert & Lucas 1997a, b, 1998a, b; 2000; 2002b; Hunt *et al.* 1998a, b;

Lucas 1998; Lucas & Heckert 2000; Lucas *et al.* 2007a) the correlations are coarse (e.g. Lucas & Hunt 1993; Huber *et al.* 1993) and subsequent refinements were often poorly supported and circular (Rayfield *et al.* 2009; Irmis *et al.* 2010).

For example, a recent paper by Spielmann *et al.* (2009, fig. 15) provided hypothesised superpositional relationships of various localities in the southwestern United States that produce the archosauromorph *Trilophosaurus* to provide biostratigraphic ranges for this taxon. However, the superpositional relationships of the localities used to construct these ranges are impossible to verify through lithologic correlation, because of the geographical separation of the outcrops. It is unclear how the relative positions of the *Placerias* Quarry, PFV 161 and the Dying Grounds (PFV 122) in Arizona were determined compared to the Kahle Quarry and Rotten Hill localities in the Dockum Group of Texas. Because the superpositional relationships of these quarries in different states cannot really be determined with the high degree of precision indicated by Spielmann *et al.* (2009), the purported composite biostratigraphic range of *Trilophosaurus* they proposed is misleading because it is unsupported by independent data.

The problems with using Late Triassic vertebrates for biochronological correlation become exacerbated when extended globally, as correlations are often based on dubious taxonomic assignments (Rayfield *et al.* 2005; 2009; Irmis *et al.* 2010). For example, Lucas (e.g. 1998, 2010) has used phytosaurs and aetosaurs to correlate the lower part of the Chinle Formation (assigned to the Adamanian lvf) with the Ischigualasto Formation of Argentina (assigned to the Ischigualastian lvf; Bonaparte 1966; Langer 2005), and also to the lower part of the Newark Supergroup in eastern North America, including the Cumnock, Pekin and New Oxford Formations (assigned to the Conewagian lvf; Huber *et al.* 1993).

Correlation between the lower Chinle Formation and the Ischigualasto Formation is based on the shared presence of the basal aetosaurines (*sensu* Parker 2007) *Calyptosuchus* and *Aetosauroides*, which Heckert & Lucas (2000, 2002b) considered congeneric. Correlation between the lower Chinle Formation and lower Newark Supergroup is based on the alleged shared presence of the phytosaur *Rutiodon* (which Lucas 1998, 2010 considers synonymous with *Leptosuchus*), the metoposaur *Buettneria* (*Koskinonodon*) and the aetosaur *Desmatosuchus*. Oddly, even magnetostratigraphic correlations between the Chinle Formation and Newark Supergroup have been based on vertebrate biochronology (e.g. Steiner & Lucas 2000, pp. 23, 803, fig. 9), with normal and reversed polarity zones aligned based mainly on biochronologic correlation of the Carnian–Norian boundary between both sections.

However, the taxonomic equivalence of *Calyptosuchus* and *Aetosauroides* is not accepted by all workers (e.g. Desojo 2004; Langer 2005; Parker 2007), and available radioisotopic dates contradict a precise age equivalence between the Ischigualasto Formation and lower Chinle Formation (Irmis & Mundil 2008). Moreover, *Rutiodon sensu stricto* may be more basal than *Leptosuchus* and more closely related to *Angistorhinus* (Hungerbühler 2001; Stocker 2008, 2010) which occurs in strata probably older than those containing *Leptosuchus* (e.g. Lucas 1998). As already discussed, there are current uncertainties in metoposaur taxonomy, and large (and usually taxonomically indeterminate) metoposaurs also occur in the Revueltian in western North America, making *Koskinonodon* a problematic means of correlating lower Chinle and lower Newark strata. Finally, the aetosaur material from the Newark Supergroup referred to *Desmatosuchus* actually pertains to *Lucasuchus* (Long & Murry 1995; Parker 2008; Parker & Martz 2010), a taxon not known from the Chinle Formation, although it is known from pre-Revueltian strata in West Texas

(e.g. Long & Murry 1995; Lucas 1998, 2010). As a result, a precise correspondence between the Adamanian, Conewagian and Ischigualastian (Lucas *et al.* 2007a; Lucas 2010, fig. 2) is not well-supported.

When biochronology, rather than lithologic correlation or radioisotopic dates, is used to determine the relative ages of strata and localities (e.g. Lucas 1993), it is inherently circular to use these relationships to support regional biochronology (*contra* Spielmann *et al.* 2009). Contrary to previous hypotheses (e.g. Lucas *et al.* 2007a), biochronologically determined relative ages, especially across geographically isolated formations, cannot be tested by more biochronology, but only through independent means such as direct lithologic correlation, magnetostratigraphy and/or absolute age determinations (Lindsay 2003; Woodburne 2006; Rayfield *et al.* 2009; Irmis *et al.* 2010).

These issues make the identification of global mass extinctions during the Late Triassic problematic. Even if the Adamanian–Revueltian turnover does represent the synchronous extinction of multiple taxa, is it a global event? Unfortunately, precisely correlating the Adamanian–Revueltian turnover to other parts of Pangaea is currently unfeasible. Until the biostratigraphic data for PEFO become more robust, biostratigraphic range data at least as detailed as presented here are plotted in other parts of the world, and radioisotopic dates become sufficiently abundant to precisely calibrate these range data, a compelling case cannot be made either favouring or discounting globally synchronous mid-Late Triassic extinction events (*contra* Benton 1994b; Lucas 1994; Hunt & Lucas 2004).

6. Conclusions

Detailed lithostratigraphic and biostratigraphic work in Petrified Forest National Park has determined that previous lithostratigraphic and biostratigraphic models for the park were erroneous (e.g. Billingsley 1985; Heckert & Lucas 2002a; Woody 2006; Parker 2006). In this paper and elsewhere (Woody 2006; Martz & Parker 2010) it is demonstrated that there is probably no regional Tr-4 unconformity, and that a faunal turnover hypothesised to occur at this interval (e.g. Long & Ballew 1985; Hunt & Lucas 1995a) actually occurs higher in the Sonsela Member, with little overlap between putative index taxa of the Adamanian and Revueltian biozones. Both the Adamanian and Revueltian biozones are Norian in age, and the Revueltian biozone is probably also partially Rhaetian. It is also noted that a floral turnover may coincide with the faunal turnover. Moreover, these turnovers may coincide with both the onset of increasing aridity in western North America and the Manicouagan bolide impact. The available data only weakly support an extinction within western North America, but do emphasise the potential importance of localised climatic changes in driving local fauna change. The available data are completely ambiguous about the presence or absence of globally synchronous mass extinctions during the Late Triassic.

At least based on the available data, the Adamanian–Revueltian faunal overturn did not have a noticeable impact on overall dinosauromorph size, diversity or prominence within the terrestrial ecosystem of the Late Triassic Western Interior (Irmis *et al.* 2007b; Nesbitt *et al.* 2007), although the impact on dinosauromorph alpha taxonomy cannot currently be assessed. The detailed and accurate provincial biostratigraphic data provided here lays the groundwork for more detailed discussion of possible Late Triassic extinction events and the tempo of evolution for various groups, including the dinosaurs.

7. Prospectus

This work is ongoing, and current data and interpretations are preliminary. Detailed mapping and measured sections of the Chinle Formation in PEFO not only allow for the precise stratigraphic placement of collected fossils and determination of taxon ranges, but also make it apparent where gaps in our knowledge exist. Future work will focus on prospecting beds where fossil data are missing or poor, in an attempt to further elucidate ranges of taxa and to test for hypothesised biotic reorganisations. A detailed geological map (Raucci *et al.* 2006; Martz & Parker 2010) allows future workers to systematically locate and prospect poorly explored beds with a higher chance of success. Also needed is a detailed palynological study building upon the work of Litwin *et al.* (1991), to test proposed palynological zonations and to confirm whether or not the floral overturn occurs at the same level as the faunal overturn, as well as palaeomagnetic and radioisotopic age data to provide independent correlation to the marine time scale (Irmis *et al.* 2010).

This paper is an attempt to provide the first step in developing a detailed provincial biostratigraphy for the Chinle Formation of northeastern Arizona and to provide accurate stratigraphic ranges of taxa for a single study area utilising detailed stratigraphic sections, in conjunction with field mapping and precise relocation and documentation of fossil occurrences. Comparison of these data with similarly compiled provincial biostratigraphies will test the applicability of nonmarine fossil vertebrates for Late Triassic biochronology, although we also realise the necessity of calibrating data points and testing for synchronous biostratigraphic boundaries with other independent means of age control such as radioisotopic dating (McKenna & Lillegraven 2005, 2006; Irmis *et al.* 2010).

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9. References

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